Technical Report No. 27

THE GROWTH AND PHENOLOGY OF METROSIDEROS IN HAWAII

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U. S. International Biological Program

August 1973

ABSTRACT

The growth and phenology of three principal varieties of Hawaiian Metrosideros were examined. All varieties have an annual flowering cycle extending over several months, usually peaking in spring or summer. The peaks of different sympatric varieties are distinct from each other. The adaptive value of periodicity in flowering may relate to reproductive isolation of different potentially cross-breeding varieties. Fruit development lasts up to one year with dehiscence of capsules occurring in the winter. Vegetative flushing of individual branches occurs twice per year in two varieties and once per year in another but is often multiphasic within a tree. A peak flushing precedes peak flowering, and subsequent flowering peaks may coincide with more flushing, if any. The growth of the trunk is continuous on all sites and is not correlated with the phenology of the tree or rainfall pattern.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The periodic growth phenomena of flowering, fruiting, budding (bud formation), flushing, leaf fall, dormancy of meristems, cambial activity, and the differentiation of internal structures are not as well known for tropical plants as for temperate ones. This is particularly true for forest species. The times of initiation, duration, and termination of these phenomena, as correlated with seasonal climatic changes, constitute a phenological record, each distinguishable phase within a life cycle being called a phenophase (Lieth, 1970).

Hawaiian Metrosideros (Myrtaceae) belong to the Metrosideros collina group found throughout the lowland or montane rain forests of high islands of the Pacific (Dawson, 1970). In Hawaii although several species have been named, it has been suggested that only one polymorphic subspecies, Metrosideros collina (Forster) A. Gray subspecies polymorpha (Gaud.) Rock, is represented, for which numerous varieties and forms have been described (Rock, 1917 and Skottsberg, 1944). The species has a broad ecological amplitude throughout the major islands of the Hawaiian chain. It is the commonest woody species of the montane rain forest and extends into drier regimes at all elevations from sea level to 2600 m.

This is the first comprehensive growth and phenological study of a native Hawaiian species. The purpose is:

(1) to describe morphological aspects of the species.

(2) to compare the growth and phenology of individuals of different varieties in different climates.

(3) to estimate the growth potential and life span.

(4) to determine the rate and periodicity of cambial activity.

(5) to estimate the role of Metrosideros' phenology in the ecosystem.

Phenological studies are significant in any ecosystem analysis. Many animal species are dependent on Metrosideros (Carlquist, 1965, Swezey, 1954, and

Zimmerman, 1948). The phenophases of a dominant forest species are interrelated to the phenologies and life cycles of these animals. Phenophases can determine food availabilities and can alter the microenvironment throughout the year for animals and plants.

Many of the recent papers on tropical phenology mention the adaptive advantage of particular phenological responses both to the plant species and other biological components in a given system (Daubenmire, 1972; Janzen, 1967; McClure, 1966; Smythe, 1970; and Snow, 1965).

In regard to Metrosideros, Baldwin (1953) noted the times of flowering peaks of Metrosideros in his study of bird populations in Hawaii Volcanoes National Park. The phenology of the New Zealand Metrosideros umbellata was recently described (Wardle, 1971). A number of papers by Dawson (1967, 1968a, 1968b, and 1970) discuss the morphology of New Zealand Metrosideros. Its role on recent lava flows in Hawaii has been studied, and some details on its growth aspects were given (Doty, 1967; Eggler, 1971, and Smathers, 1972).

METHODS

Selection of plots--Tree sites were selected in Palolo Valley on Oahu (TABLE 1 and FIG. 1), one of the valleys in the Koolau mountains north of Honolulu, Hawaii. These were at similar altitudes but different climatic regimes. The deeply dissected valley runs from the crest of the range toward the sea for a distance of 3 Km. There is an annual rainfall gradient from 3800 mm at the head to 750 mm at the mouth of the valley. One site (plots 0 and 1) is on the low central ridge that divides the valley. The second site (plot 2) is higher on the ridge to the west of Kaau crater, the trees located next to the trail that traverses the narrow ridge to the summit of the range. The third site (plots 3 and 4) lies 0.8 Km due south of the first site on Mauumae Ridge in a much drier area on the Lanipo trail.

TABLE 1. Plot locations and characterizations. Plots 0 to 4 on Oahu, 6 to 14 on Hawaii in Hawaii Volcanoes National Park.

Island	Plot number	Specimen number	Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type[a]	Substrate[a]	Observation period	Estimated avg. annual rainfall[b] (mm)
Oahu	0 and 1	1-20	Palolo Ridge	420 m	21°19'30"	157°47'	Open Metrosideros-Acacia-Dicranopteris humid montane forest	Humic latosol	6/70 to 11/71	3000
	2	21-30	Kaau Crater	550 m	21°20'	157°47'	Open Metrosideros humid montane forest	Humic latosol	7/70 to 11/71	3500
	3 and 4	31-50	Mauumae Ridge	396 m	21°18'40"	157°47'	Open Metrosideros-Acacia tropical summer-dry forest	Brown loam	10/70 to 10/71	1500
Hawaii	6	61-70	Kalapana-Kamoamoa	15 m	19°18'	155°05'	Metrosideros-Diospyros tropical summer drought savanna	pahoehoe	3/71 to 3/72	1800
	7	71-80	Mauna Loa Summit Trail	2135 m	19°31'	155°25'	Globous shrub-scattered Metrosideros cool summer dry scrub	weathered aa	11/70 to 3/72	1200
	8	81-90	Kipuka Ki	1256 m	19°27'	155°19'	Mixed Metrosideros-Sapindus-Acacia summer dry forest	pahoehoe-deep ash	1/71 to 3/72	2400
	9	91-100	Tree molds	1220 m	19°26'	155°18'	Open Metrosideros-lichen-shrub summer-dry-humid transition	pahoehoe-thin ash	11/70 to 3/72	2400

TABLE 1. (Continued) Plot locations and characterizations

Island	Plot number	Specimen number	Location	Elev.	Lat.(N)	Long.(W)	Vegetation/Climate type[a]	Substrate[a]	Observation period	Estimated avg. annual rainfall[b] (mm)
	10	101-110	Highway 11	1228 m	19°26'	155°16'	Open Metrosideros-Sadleria fern humid-summer-dry transition	pahoehoe-thin ash	1/71 to 3/72	2500
	11	111-120	Thurston Lava Tube	1195 m	19°25'	155°15'	Closed Metrosideros-Cibotium fern humid montane rain forest	moderately deep ash	11/70 to 3/72	3000
	12	121-130	Hilina Pali Rd.	1028 m	12°22'	155°18'	Metrosideros-native shrub warm summer dry	pahoehoe-ash	11/70 to 3/72	2100
	13	131-140	Hilina Pali	725 m	19°22'	155°18'	Open Metrosideros-Andropogon warm summer dry grassland	aa	11/70 to 3/72	1300
	14	141-150	Mauna Loa Strip Rd.	1570 m	19°28'	155°21'	Open Metrosideros-Sophora-Dodonaea summer dry forest	aa	3/71 to 3/72	1500

[a]Adapted from Doty and Mueller-Dombois (1966).

[b]Adapted from Blumenstock and Price (1967).

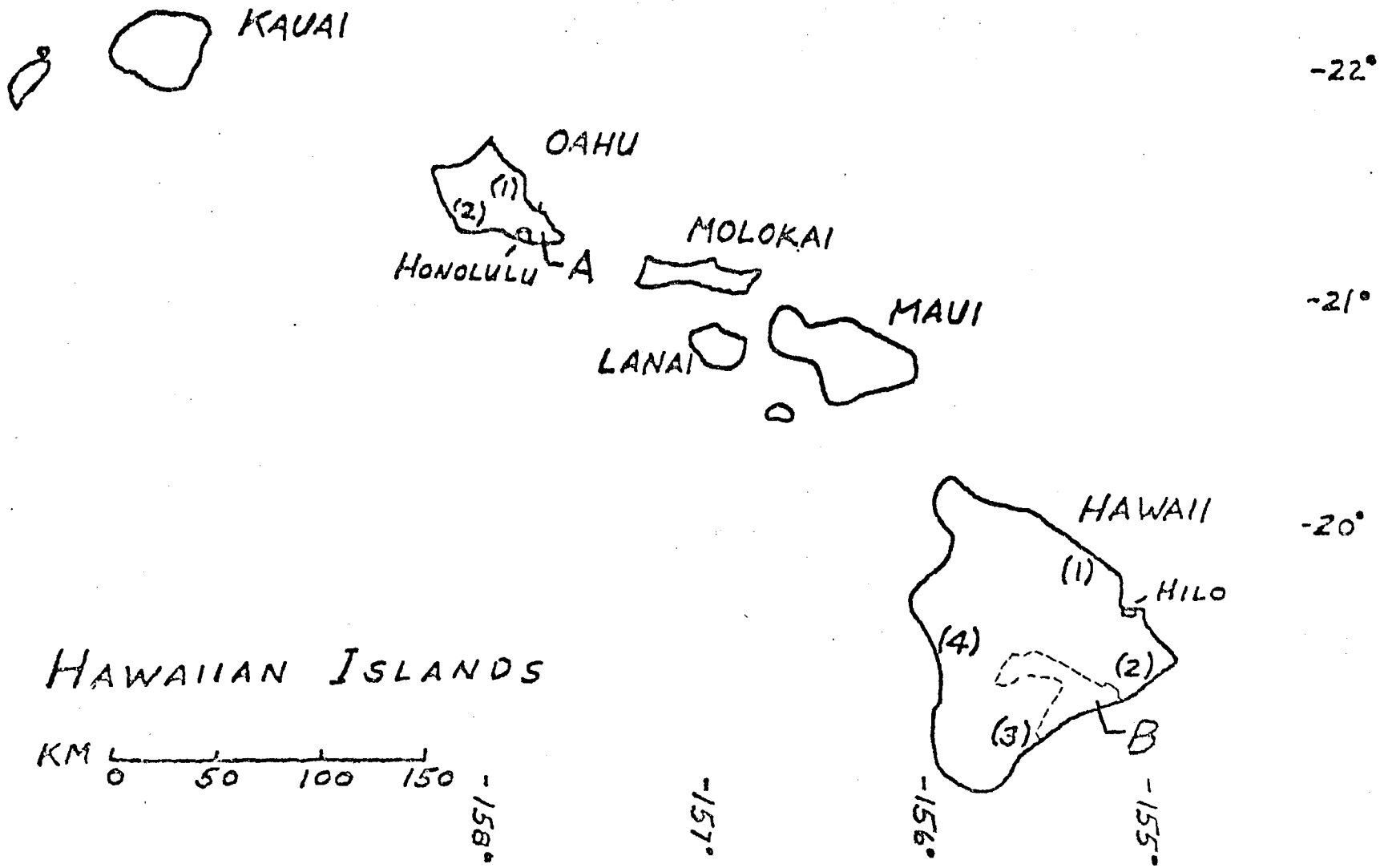

FIG. 1. The Hawaiian islands. On Oahu, A is Palolo Valley, (1) the Koolau mountains, (2) the Waianae mountains. On Hawaii, B is Hawaii Volcanoes National Park, (1) Hamakua district, (2) Puna district, (3) Ka'u district, (4) Kona district.

These sites were selected because they were accessible, and they included diverse forms of the two commonest varieties on Oahu, polymorpha and glaberrima.

In conjunction with the Hawaii International Biological Program and following ecological study transects previously established (Doty and Mueller-Dombois, 1966), nine sites were later selected in Hawaii Volcanoes National Park at various locations convenient to roads or trails at different elevations and under different climatic regimes. Ascending from sea level on the transects one passes through summer-drought, then humid, then summer-dry climate again. At these sites (plots 6 and 14, TABLE 1) the variety incana was most abundant. Ten trees in each plot were chosen for detailed observation for a minimum of one year. Observations were recorded at approximately monthly intervals, during the time periods indicated in TABLE 1. The total number of specimens for the 14 plots was 140, including 134 trees and 6 shrubs. They included 16 specimens of variety polymorpha, 34 of variety glaberrima, 88 of variety incana, and 1 each of varieties nuda and macrophylla (in TABLE 12).

Phenological data--Ten trees or shrubs were tagged in each plot. These were suitable for trunk measurements and represented size classes and taxa deemed to typify the plot. Two kinds of records were kept; whole tree or plot data and branch data.

For whole tree data the amount of flushing was estimated. Depending on the relative number of new flushes, flushing was recorded as none, few meant less than 5%, some meant about 5 to 25%, and many meant more than 25% of the branches on the tree were producing new shoots. The number of inflorescences visible from one vantage point were counted. More than thirty was recorded as 30+. Photographing each specimen each time data were collected for a phenological record was rejected because of the difficulty of taking pictures in the more dense stands or in rainy weather.

For branch data branches were tagged on at least two specimens in each plot, ten branches on each of three trees in the first two plots, five on all others when five was deemed a sufficient number of branches for recording phenology. Each branch was diagrammed and the number of nodes, leaves, enlarging buds, flushes, length of flushes, insect attacks, flower buds, flowers, fruits and stage of maturity, and any other phenomena of interest were recorded at each observation period.

Trunk growth data--On all tree specimens nails were driven into one or more trunks at 1.5 m height to serve as reference points for measurements of circumference. Measurements were taken at same times as phenological observations. At the first measurement loose bark was removed, and the loop at the end of the measuring tape was hooked on the nail with the tape put around the tree and over the nail. On the larger trunks, one or more extra nails were hammered in below the tape when in position to assure duplication in its placement each time a measurement was made. Circumference rather than radial growth was recorded since measurement at one level of "all radii" by means of circumference obviates the necessity of selecting a representative point to use with such a device as a dial gauge dendrometer.

Certain problems did occur. A few nails caused splitting of the bark and wood especially in smaller trunks. Some trees in wetter localities had a thick layer of epiphytes removed to expose the bark which could alter the hydration and aeration of the bark and thus initially affect the measurements. Another problem was the degree of tension to be placed on the measuring tape. At first I used a "tension handle", but this proved to be too unwieldy. I learned to gauge the appropriate tension myself, depending on the thickness, texture and compressibility of the bark. On a few trees it was difficult to estimate the proper tension even after repeated measurements. Measurements from such trees (for example, tree 134) tended to fluctuate more than the average amount.

When repeating measurements, I tried to measure each tree at the same time of

day so that temperature and transpiration conditions would be similar. Also, rainfall could alter the precision of measurement: during rains, portions of the bark could become water saturated by stem flow and increase the circumference value.

Cambial activity--Two methods of determining the activity of the vascular cambium were employed, the block method and the strip method. Blocks of bark-cambium-wood about 1 cm square on the tangential surface were removed using a hammer and chisel. Loose outer bark was first removed. A block to a depth of about 5 mm into the sapwood was extracted and immediately transferred to CRAF III fixative in plastic bottles to preserve them for microscopic examination. At least one block from one tree in each plot was collected in the above manner at each observation time. Except in rare instances the bark easily separated from the wood at the cambial zone. This slippage of the bark indicated that the cambium was active. This method exposed the tangential surface of the cambial zone so that the orientation of the vertical elements of the vascular tissues could be determined. It also revealed the thickness of the inner bark and sapwood. The block method has been considered the most accurate method of determining activity since the relative number of young xylem cells and their degree of differentiation, i.e., lignification, can be observed microscopically (Lodewick, 1928). The blocks were embedded in celloidin and sectioned for this purpose.

The strip method involved the removal of a narrow strip of bark with a knife. The slippage of the bark indicated the degree of cambial activity (Schneider, 1952). This method was most useful on smaller branches where the chisel could not be used. Both of these methods have been used by many workers for several years (Studhalter, Glock, and Agerter, 1963).

Besides direct examination of the cambium by these methods, change in circumference is an indirect measurement of cambial activity, although increases caused

by the formation of new phloem and xylem by the vascular cambium are difficult to separate from changes in circumference related to cork cambial activities and hydration of the wood and bark.

The past record of growth can sometimes be revealed from cores, discs, and sawn logs. Wood cores of 4 mm diameter were taken with a "Djos" increment borer for examination of growth rings.

OBSERVATIONS AND DISCUSSION

Leaf and Branch Growth

Budding and flushing

The fresh growth of the shoot from a bud is a flush. The process is called flushing. The last branchlet produced on a branch is termed a twig. In Metrosideros the buds involved in flushing are typically the most distal pair of axillary buds. The development of these buds occurs after the cessation of stem elongation in the flush on which they are produced. An individual bud may either enlarge to a few millimeters in diameter and then remain dormant for some months, or it may enlarge and continue to develop into the new flush without undergoing a dormant stage on some trees under certain conditions.

Typically, the bud enlarges to at least 3 to 4 mm in diameter before bud break, the opening of the bud. At this stage there are usually four or five pairs of leaves enclosed within the bud scales plus occasionally primordia of more pairs of leaves. The older leaf primordium is slightly curved, valvate to the other leaf of the pair, decussately arranged, and the blade is planar and even, not rolled, corrugated or folded. As the bud then further enlarges accompanied by the elongation of the stem itself, the leaves become imbricate.

Leaves destined to become revolute at their margins as in the varieties rugosa and polymorpha or repand as in some individuals of the variety incana do

not have revolute or repand margins until bud break. During the development of a bud the epidermis of all surfaces may form a detersile pubescence. The developing leaves within the bud in most varieties may acquire red pigments from the outer or lower leaves inward. Accompanying these developments, the bud scales enlarge.

The bud scales in Metrosideros are of two or three types arranged decussately in series. The outermost series is imperfectly developed and is variable in size and number. They are the most membranous, but yet they are the scales that may be either the most fugacious, soon falling, or the most marcescent, withering but persisting. Their color is dark reddish brown. The buds of certain trees may have this outer series of scales persisting for several months after bud break.

The second series consists of red to green to yellow scales, tightly imbricate, grading in size, with margins more or less membranous and with pellucid punctate dots scattered throughout. The bud scales seem to be the only structures in Hawaiian Metrosideros that bear pellucid puncta. This series is soon deciduous.

The third, innermost type may or may not be present. They are foliaceous transitional leaves having a petiole and may persist for a few weeks at the base of flush after bud break. There is always but one pair of this type. After falling they leave reniform bud scale scars which are also transitional in form between the curved linear form of the other bud scale scars and the more circular leaf scars. I noted one node having both a leaf and a bud scale of this transitional type.

The size and shape the bud attains before bud break is quite variable among the different varieties and forms of Metrosideros. It may be rounded and blunt or flattened and pointed (FIG. 2) and may range from one to three centimeters in length. The thickness of the bud scales also varies in direct proportion to the thickness of the leaves of the variety in question. The bud scales become angled along their length at bud break and are pushed back by the emergence of the stem

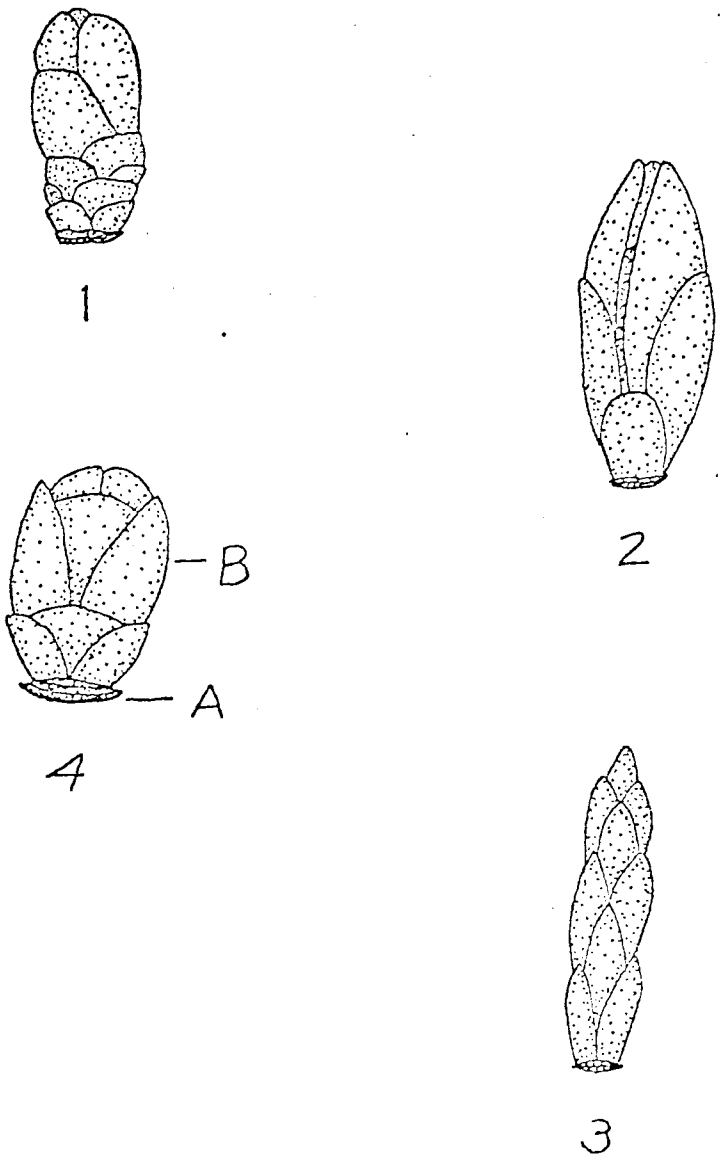

FIG. 2. Buds prior to bud break showing two types of scales; the basal membranous type (A) and the more conspicuous type (B) above. 1--var. polymorpha, Waianae mountains; 2--var. glaberrima, Waianae mountains; 3--var. tremuloides, Koolau mountains; 4--var. incana, Ka'u district. 2X.

and leaves. They may rapidly abscise as the twig elongates.

In the variety macropus the scales of the second series persist for at least one year, remaining quite chlorophyllous and it was on this basis that Hooker and Arnott considered it as a distinct species, M. macropus (Rock, 1917).

In a few trees, some tremuloides for example, there may be considerable elongation of the internodes in the region of bud scale attachment both below the lowest scale and in between each pair of scales. Sometimes this region will become 2 centimeters in length before the leaves even emerge. In most buds, though, this area remains the same length as in the bud, up to 6 mm long.

Prior to bud break the number of bud scales may be fewer, the same as, or greater in number than the leaves produced in the subsequent shoot. Of 98 buds collected from the high elevation form of variety incana along the Mauna Loa Summit Trail and subsequently dissected, 34% had more bud scales than leaves in the bud, 12% had the same number of scales as leaves, and 54% had fewer scales than leaves. The number of scales in one case was 18. In New Zealand Metrosideros there may be up to 16 (Dawson, 1968b).

After bud break the internodes elongate and the leaves begin to expand and open outwardly from their fastigiate position. FIG. 3 diagrams the growth of some incana leaves in length and their changing axillary angles through time, each time superposing the pair on the same twig at the same position. The tip of the leaf scribes a parabolic curve in this fixed position on the diagram.

The flush elongates into a twig from 2 to several cm (commonly about 5 cm) in length. The leaves expand uniformly so that the mature leaf is roughly proportional to the others from its size at bud break, throughout flushing, to cessation of elongation. A most distinctive feature of all varieties is that the lower leaves are the largest. There is a gradual decrease in size to the upper smallest leaves.

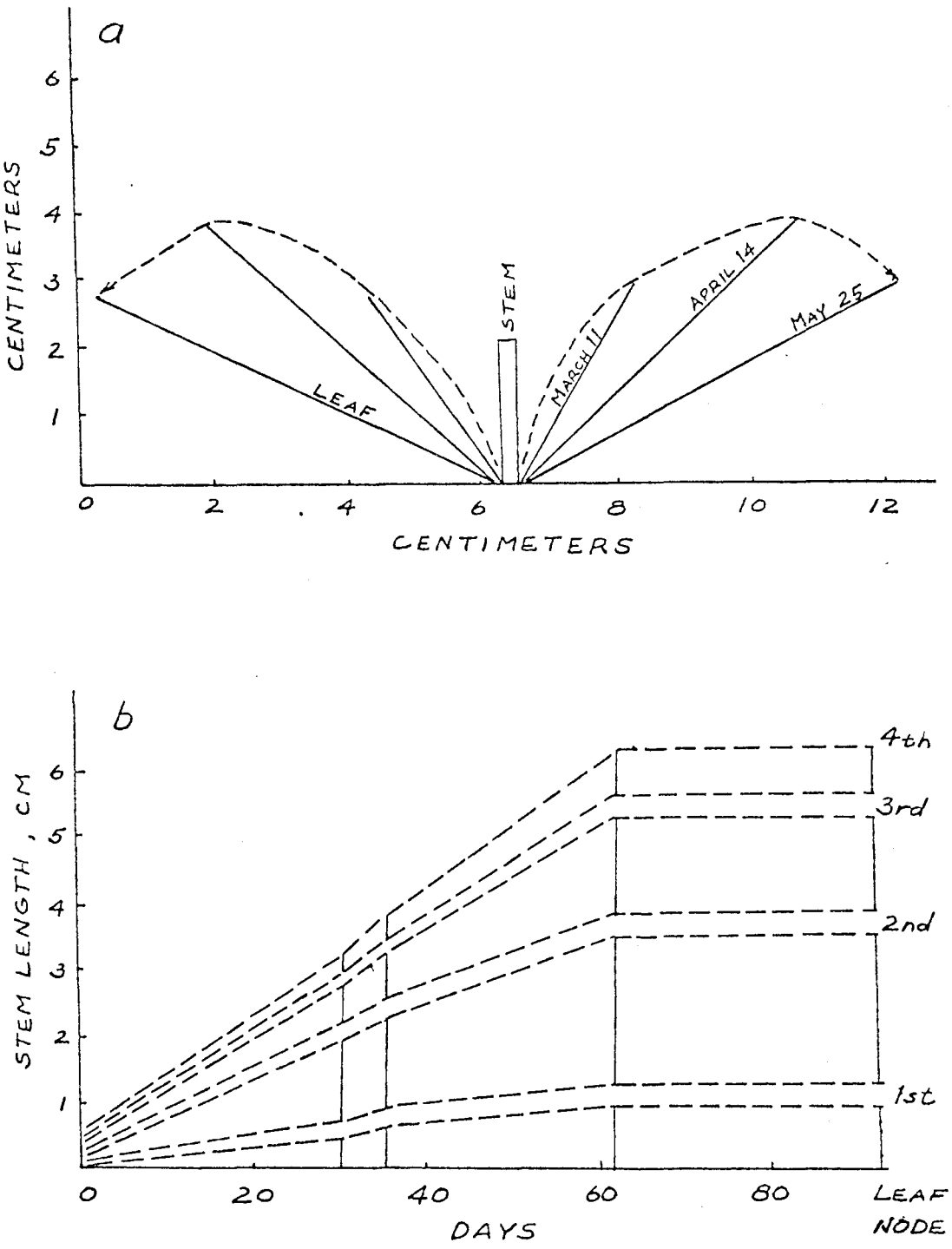

FIG. 3. Growth rates in leaves and twigs in the variety incana. In a, the changing angle and length of a pair of basal leaves of a flush; in b, a vegetative flush, the vertical lines represent the relative lengths of the internodes between the bud scales at the base and the lowest four leaf bearing nodes during the time elongation is occurring.

Mode of Branching

Mode of branching refers both to the spatial relationship of one branch to another and also the phenological aspects of growth and their coordination. Manifold growth is one mode of branching referring to asynchrony of branching. Koriba (1958) refers to "stockwise manifold growth" where individual trees of the same species differ in timing, and "branchwise manifold growth" with various branches budding and flushing at different times on the same tree. Metrosideros has both types of manifold growth, but there is usually a fair degree of coordination within a single tree with a degree of asynchrony of the development of the new twigs varying from a few days to several weeks. Flushing is often conspicuous with the new flushes having a contrasting color to the mature foliage so definite flushing peaks can be easily observed.

By Koriba's system, Metrosideros is evergreen-lateral-manifold in mode of growth. For any one branchlet, this term can be expressed as evergreen-lateral-intermittent. Even if one did not periodically observe the actual growth of a branch, the fact that the leaf size is not uniform, the length of internodes is unequal, bud scales are present, and there are abrupt color and texture changes in the epidermal and cortical layers of the twigs, would indicate that this was a tree bearing branches of intermittent growth.

Metrosideros has sympodial, lateral growth. This means that the shoot apex regularly aborts and then one or more axilliary buds forms a new twig or twigs. This conforms to Dawson's (1968b) Group A vegetative bud pattern. This is not analogous to the shoot tip abortion in Syringa vulgaris where the terminal bud and a few pairs of tip leaves dry up and fall off (Garrison and Wetmore, 1961). The two paired buds just below the apex give rise to new branches that appear to be dichotomous. This is called substituting growth (Koriba, 1958) since a terminal bud's growth potential is substituted for by an axillary bud. Not uncommonly the

twig dies back further and axillary buds lower down the twig grow substitutively. Eight types are diagrammed in FIG. 4.

In TABLE 2 the frequency of the various types of branching is given. They may occur on the same tree although all types were not recorded on a single branch. Of 757 branches examined, 361 (47.6%) formed a single new shoot, 321 (42.4%) produced a pair of new shoots, and 75 (10%) formed three or more.

On rare occasions a resting terminal bud does develop at the shoot apex. Of the 155 branches tagged, one had a terminal bud that formed in January and opened in June 1971. When it did open, the flush did not elongate and the leaves were rudimentary. On a branch from Kauai (Lamoureux 4458) there was terminal bud. On one tree (Porter 63) in plot 6 there were several branches on one tree having terminal buds which developed into vigorous shoots. This particular tree had a different flowering time than the other trees in the plot.

To determine if paired buds have an equal potential in terms of producing determinate shoots of the same length, I examined those that formed false dichotomies during the observation period. The numbers of nodes in each twig of a twig pair are expressed as ratios in TABLE 3. Branches of the variety incana produce the greatest range, and show that the number of nodes in the two twigs of a false dichotomy are not equal. The average number of nodes in the variety incana is more than four, in polymorpha less than four. In glaberrima three or four nodes are common except in a small leafed imbricate form represented by shrub 46.

Types of shoots

Metrosideros forms three kinds of shoots: determinate or short shoots, indeterminate or long shoots, and epicormic shoots. This is modified from Kozlowski's system of shoot classification (1971).

Determinate shoots--This kind of shoot is preformed in the axillary bud. When

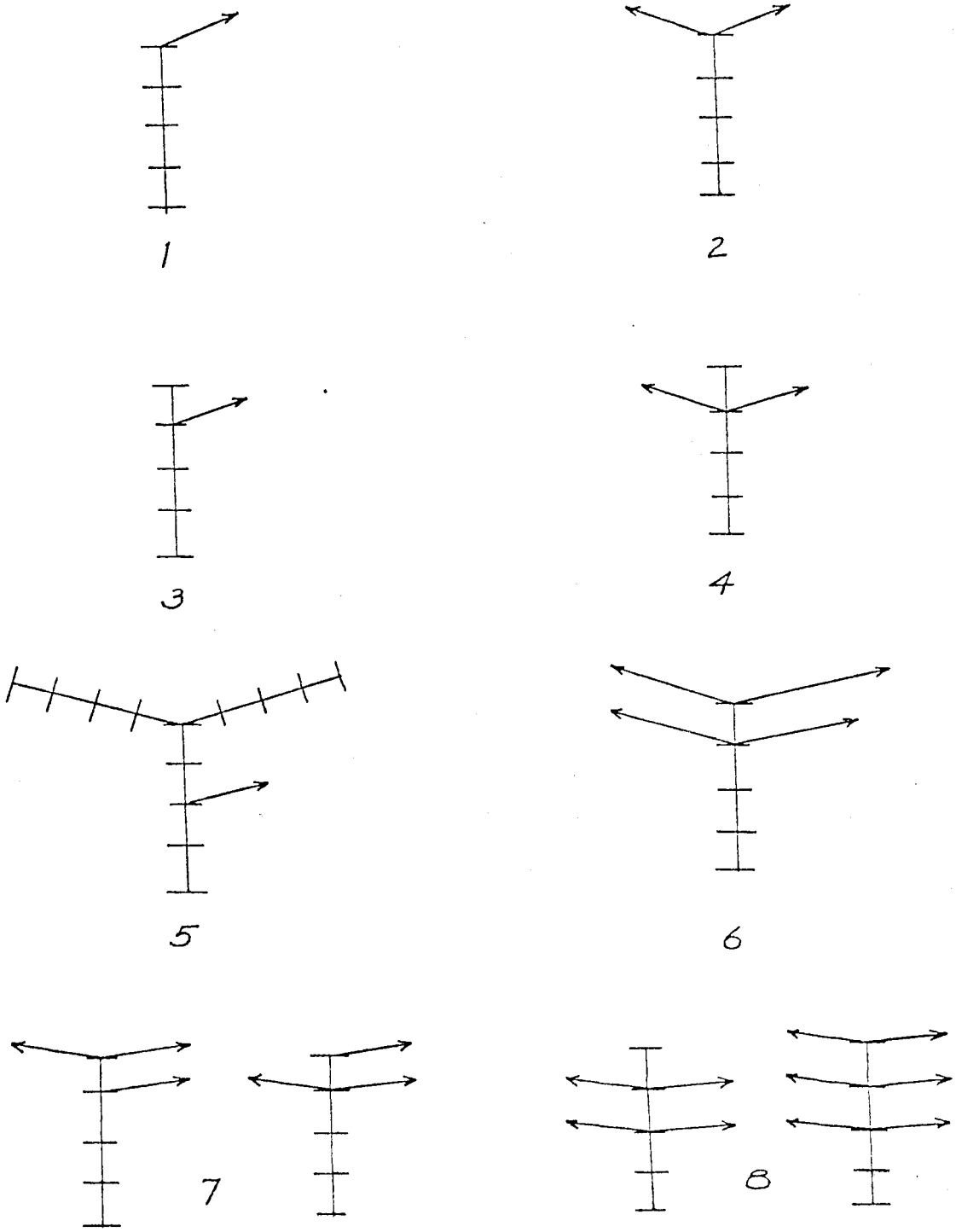

FIG. 4. Mode of branching types. Arrows show new branches. Dashes show position of nodes on old branches.

TABLE 2. Frequency of the different branching types shown in FIGURE 4. The data are derived from branches of varieties polymorpha and glaberrima on Oahu and variety incana on Hawaii.

Type	Oahu		Hawaii		Total
	Number	per cent	Number	per cent	per cent
1	100	29.1	171	41.4	35.8
2	142	41.3	136	32.9	36.7
3	24	7.0	21	5.0	5.9
4	18	5.2	25	6.1	5.7
5	24	7.0	21	5.1	5.9
6	5	1.4	7	1.7	1.6
7	25	7.3	25	6.1	6.7
8	6	1.7	7	1.7	1.7
Total	344	100.0	413	100.0	100.0

Total branchings = 757

Total branchlets = 1267

TABLE 3. Numbers of nodes per twig pair, expressed as ratios.

Ratio	Variety						
	incana	polymorpha	glaberrima				
			No. 46	47	48	49	50
2:2		1					
2:3						1	
2:4	1	1					
2:6	1						
3:3	2	8			1	2	4
3:4	5	3		1		2	
4:4	5	10				1	2
4:5	2						1
4:6	5					1	
4:7	1						
5:5	7	2					2
5:7	1						
6:6	1		1				
6:7	5		1				
6:9							1
7:7	4						
7:8	3		1				
8:8			1				
8:9	2						
9:9	1						
Total	46	25	4	1	1	7	10
Avg. ratio of nodes	4.93 / 5.76	3.48 / 3.68	6.75 / 7.25	3/4	3/3	3.1 / 3.9	3.8 / 4.8

flushing occurs, a short shoot with an aborted apex and four or five nodes is produced. The elongation phase of flushing lasts about two months or less. This is the predominant shoot type comprising most of the whole shoot system.

Indeterminate shoots--Although only a few of the flushes observed on tagged branches were indeterminate, in other areas outside the study plots I have seen a number of specimens bearing long, indeterminate shoots. When such a shoot continues to grow from the apex of the shoot derived from the axillary bud, it is called a sylleptic shoot. If during the same year just following hardening off of a determinate shoot, more determinate shoots flush from axillary buds, these "late" shoots are called proleptic shoots. One tagged branch produced an indeterminate shoot, no. 120-3, which elongated continuously from May to September, 1971. Ultimately it was 18 cm long and had 11 nodes and 22 leaves. This kind of shoot appears to have been formed in two flushes because the leaves are graduated in size in two series. In this kind of shoot one often finds smaller leaves than normal for the variety, less than 0.5 cm in length and breadth.

Whether the shoot is formed from a determinate or indeterminate flush does not alter the basic sympodial growth pattern. Upon cessation of growth the apex remains undeveloped and subsequent flushes develop from axillary buds. Determinate flushes usually complete elongation within two months, indeterminate flushes take longer. With the determinate flush usually but one, two, or three axillary buds form subsequent flushes. Indeterminate flushes may produce several such flushes from the buds near the tip.

The variety imbricata produced by Rock (1917) seems to be a manifestation of this growth form. His variety was admittedly like the variety polymorpha (syn. typica) yet differed by having long shoots with imbricate leaves. I have encountered this form in many varieties. From the imbricate incanas growing along the Footprints Trail in the National Park, a few such shoots were collected and

measured. One was 12.5 cm long with 17 nodes, another 17.5 cm long with 30 nodes, and a third 30 cm long with 35 nodes. The longest leaves are at the base, but another series of larger leaves is produced higher on the flush. Commonly there are two peak modes of growth in such a flush.

Other such imbricate forms I have examined were collected by C. Corn on Kauai. They include one 42 cm long with 35 nodes, one 24 cm long with 44 nodes, one 62 cm long with 33 nodes (being less imbricate but still having two modes of growth), and one 17 cm long with 19 nodes. Also she collected some from a small-leafed glabrous variety on Kauai. One was 18 cm long with 20 nodes.

The fact that this type of indeterminate growth form is infrequent but occurs gregariously and in several varieties suggests an environmental cause. On Oahu they occur most frequently on the windward side of the mountains at lower to intermediate elevations. On Hawaii they have been found at all elevations but more frequently in the drier, intermediate elevations. In the Footprints Trail area on the island of Hawaii there are areas with over half the trees possessing the imbricate form. These trees are apparently not producing regulators inhibitory to growth as occurs in determinate shoots or only on a delayed basis. What soil or climatic factors are contributing to this is unknown.

Epicormic shoots--Epicormic shoots are those shoots which develop from buds of the trunk and branches some distance back from the growing apex. Some of these are latent or slow growing buds having bud traces to the pith. Some of these may be adventitious buds that lack bud traces (Kozlowski, 1971). Several dozen epicormic shoots may arise from one area, a burl, but within a year or so most die and abscise.

Most epicormic shoots in Metrosideros are easily recognized since they are not ascendent to the stem to which they are attached. The branch angle often approaches 90 degrees. If there are numerous such shoots attached to a burl, then

the shoots will diverge from the perpendicular. On horizontal branches they are most often attached to the upper side of the branch and grow straight upward.

Most of the trees in the plots exhibited epicormic shoots. Twenty per cent of the trees at the Palolo Valley sites had many epicormic shoots, and 40 per cent had a moderate number. On the island of Hawaii, epicormic shoots occurred at all sites but are less prevalent at the higher elevations. On those trees with many epicormic shoots, such shoots arise all the way from the trunk base to the outer branches. Sometimes they bear the bulk of the leaves in the crown as in half of the trees at the Thurston Lava Tube plot. Epicormic shoots form when apical dominance of the foliage crown declines from senescence, disease, insect attack, and sudden defoliation by volcanic cinder fall.

The epicormic shoot is the only kind of shoot, other than the seedling, which may exhibit juvenile characteristics in Metrosideros. The nearer the epicormic shoot arises to the root system, the greater the tendency toward juvenility. One example is a tree of the variety polymorpha having dark green adult foliage and light green pubescent young determinate shoots; the young basal epicormic shoots had large, glabrous, bright red leaves. Another example is a shrub of the variety glaberrima having small, light green, imbricate leaves; the basal epicormic shoots had long internodes and dark red leaves four times the size of the adult leaves. The juvenile leaves in these cases resembled not only seedling leaves but the leaves of determinate flushes of other varieties.

The paradox seems to be that the shoots borne on the oldest part of the tree, the base of the trunk, are the most juvenile in character. Steward (1968) said, "The development of a given leaf primordium may well be a function of the morphogenetic environment in which it develops which may also be, in turn, a progressively changing function of the age of the shoot." The base of the plant containing some of the tissues of the seedling plant even after many years may be still

juvenile in character. An important factor, though, is that the dormant buds at the base of the trunk are far removed from the apical portions of the tree where the most active production of hormones is taking place.

Measurements of extension growth

Flushes could be measured approximately monthly on tagged branches. TABLE 4 gives the mean values for rates of elongation of flushes on different varieties at different elevations. Specimens 21 and 22 were combined since they were small shrubs of the same form growing near each other. The branches on trees 1, 86, 117, and 120 were epicormic shoots and grew more rapidly than other flushes at the same sites. Two flushes elongated for over three months and these were indeterminate shoots. There are variable rates between twigs on individuals, indicated by the sample standard deviation (S.D.) and between individuals in the same plot, e.g., trees 133 and 136.

Twigs on shrubs 46, 47, 48, and 50 growing close together had similar rates the first month, but different rates through the second month. On the average twigs attain a length of 50 mm, but there is no correlation between rate of elongation and elevation as in the variety incana.

The factors which seem most important in affecting the rates of elongation are the kind of shoot, the age or size of the specimen, the variety, the amount of branching or twigginess.

The growth rates of eipcormic shoots were similar to those seedlings I have observed. They cannot be considered in the overall increase in height of a specimen since they are not part of the normal branch system but are a type of regenerative shoot on senescent or damaged trees.

None of my specimens are seedlings (less than 1 m tall), but they must range over many different ages. As a tree matures the vigor and rate of growth generally

TABLE 4. Twig elongation (mm per month). Individual twigs are recorded during the time they were elongating. For example, on tree 1, 48 twigs were measured the first month, 32 of them were still growing the second month and only 2 were still growing the third.

Variety	Elevation (m)	Specimen number	Observation period	First month			Second month			Third month		
				Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
polymorpha	420	1	7/70 to 9/71	40.8	19.7	48	12.0	7.8	32	7.5	2.5	2
		17	7/70 to 9/71	30.3	16.2	32	8.6	5.9	16			
	396	49	10/70 to 10/71	20.0	8.5	12	5.0	0	3			
glaberrima	420	16	7/70 to 9/71	43.8	18.8	29	26.8	21.4	18	10.0		1
	550	21-22	7/70 to 9/71	22.6	9.4	44	11.3	10.1	16			
	396	46	10/70 to 10/71	38.3	14.8	21	13.3	6.8	6	25.0[a]		1
		47	10/70 to 10/71	44.1	16.8	16	12.5	5.0	4			
		48	10/70 to 10/71	49.6	18.9	11	35.0	14.2	2			
		50	10/70 to 10/71	42.8	19.7	9	40.0		1			
incana	15	63		28.0	6.8	10	17.0	7.6	5			
		66		67.1	27.6	31	15.7	4.5	7			

TABLE 4. (Continued) Twig elongation (mm per month)

Variety	Elevation (m)	Specimen number	Observation period	First month			Second month			Third month		
				Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
incana	725	133	1/71 to 1/72	39.3	11.7	7	11.0	8.9	5			
		136	3/71 to 1/72	52.1	14.1	12	31.3	11.8	4			
	1025	125	1/71 to 1/72	56.9	38.8	13	5.0		1			
		130	1/71 to 1/72	26.9	5.9	8	7.0	4.5	5	7.5	3.5	2
	1195	117	1/71 to 1/72	47.0	22.5	23	21.3	6.4	12	20.0		1
		120	3/71 to 1/72	70.0	26.0	3	31.7	5.8	3	25.0[a]		1
	1220	99	1/71 to 1/72	30.0	3.5	5			0			
		100	1/71 to 1/72	24.1	5.8	11	7.5	4.2	6			
	1228	104	1/71 to 1/72	21.5	7.7	13	27.2	9.1	7			
		106	3/71 to 1/72	25.6	10.8	8	14.2	5.8	6	5.0	0	2
	1256	86	1/71 to 1/72	48.3	28.9	3	16.7	7.6	3			
		89	1/71 to 1/72	37.8	15.4	9	36.0	8.2	5			
	1570	142	3/71 to 1/72	37.2	17.7	16	32.0	18.6	5			
		147	3/71 to 1/72	46.7	5.8	3	12.5	3.5	2			
	2135	76	1/71 to 1/72	27.0	6.7	5	8.3	5.8	3	5.0		1
		78	1/71 to 1/72	17.0	2.8	5	5.0	0	2	5.0		1

[a] A twig with indeterminate growth.

decline, the lengths of internodes decrease, while the number of short determinate shoots increases (Wilson, 1970). In the normal shoot system, there is a correlation of internode length with leaf size. With longer internodes there are larger leaves, and with shorter internodes there are smaller leaves with shorter petioles. These correlations in growth contribute to the characteristic form of certain varieties of Metrosideros, a rather geometric orderliness of the leafy branch tips, from the short internodes with the rigidly affixed small leaves of the variety rugosa on the one extreme to the long internodes with the long-petioled large leaves of the variety macropus on the other.

The variety incana at high elevation and in the small trees at 1220 and 1228 m elevation had slower rates comparable to two trees of variety polymorpha with regular determinate shoots. In general though, incana and glaberrima have faster rates than polymorpha.

Shrubby varieties such as tremuloides, in its typical form, are heavily branched and twiggy with a dense crown. The rates of elongation and the lengths of the flushes formed are similar to the tree species, some less as in the case of the common summit form of glaberrima with a maximum twig length of 55 mm and some more as in a glabrous form with affinities to tremuloides with a maximum twig length of 75 mm.

Often optimal conditions for vegetative growth are optimal for insect activity and hence for insect damage to new growth. Damage occurred at all sites. On the tagged branches 445 buds and twigs were attacked by various insects that either chewed, bored or produced galls in them. These attacks occurred among 747 flushes. The leaf galls probably reduced the photosynthetic capacity of the leaves, and the stem galls weakened the branchlets increasing the amount of wind breakage.

Phenology of leaf production and leaf fall

Leaves are produced during vegetative flushing, relatively rapid processes occurring during much of the year. Leaf fall is seldom a sudden process in Hawaiian Metrosideros. The numbers of fallen leaves, counted as missing from the previous observation time, varied from branch to branch, continuing throughout the year. The color change before abscission were quite apparent. The leaves first turned light green, then red or yellow, and finally brown before falling.

On a particular branch there were two sequences of leaf fall. On the newest twigs a pair or two of leaves abscised in the first few months after flushing. Those leaves that persisted longer remained on the tree probably two to three years. On most specimens the maximum age of leaves was three years. The sudden fall from any one branchlet usually was coincident with the production of a new flush distal to it on the same branch.

The age of the leaves can be deduced once the frequency of flushing is determined for a particular plant. For example, if a tree produces no more than one flush each year, leaves borne on a branchlet two bud scars back from the tip are at least two years old. On many branches the average life span for a leaf is two years. Exceptions occur in the variety nuda where a high percentage of three and four year old leaves are persistent, and in some incana trees growing at 2000 m elevation on Mauna Loa where leaves frequently persist up to 15 years. The branches to which these old leaves were attached were 2 cm in diameter.

The retentiveness of a leaf is related to the development of the immediate axillary buds. Development of the bud into a flush hastens leaf fall at that node. Rapidly growing seedlings also have greater retentiveness of leaves.

Typically the first leaves to fall in all varieties are the distal and proximal leaves of the newest shoot. In those shoots with short basal internodes, the basal leaves abscise within a few weeks of maturation of the twig. The distal

leaves abscise either following tip die-back that accompanies flushing from buds located at the second or third node or from crowding by bud enlargement at the distal node itself.

Offsetting leaf fall is production of leaves in the new shoots. The variety incana has one flush per year while varieties glaberrima and polymorpha have two. Whether this is in part a different climatic response is not known. In variety polymorpha with distinct times of flushing, leaf fall seems to accompany production (FIG. 5). In varieties with less regular flushing, leaf fall is irregular.

Reproductive Growth

Type, form, and position of inflorescences--The inflorescence of Metrosideros consists of a single axis with a variable number, often eight, of decussately arranged cymules, of three sessile or pedicellate flowers terminating in a single cymule or a dichotomous pair. The cymules consist of two axillary flowers and one terminal flower, all subtended by bracts. The amount of congestion of the flowers within the inflorescence is variable, depending on the length of peduncle and pedicels (FIG. 16). The inflorescences are produced in leaf axils where single vegetative buds would otherwise be found.

One form of the inflorescence in Hawaiian Metrosideros according to Dawson's classification (1968) is open, that is, a vegetative bud is formed at the tip of the inflorescence from which a continuing shoot will form after a period of dormancy. The fruits developed from the inflorescence often persist after the new twig is formed above it so that it resembles an intercalary inflorescence. Occasionally more than one vegetative bud terminates an inflorescence but more than one has not been observed developing. Open inflorescences were found on 8 of 23 specimens having tagged branches with flowers on them. When they do develop near the tip of the most recent twig, the process is called acranthous flowering.

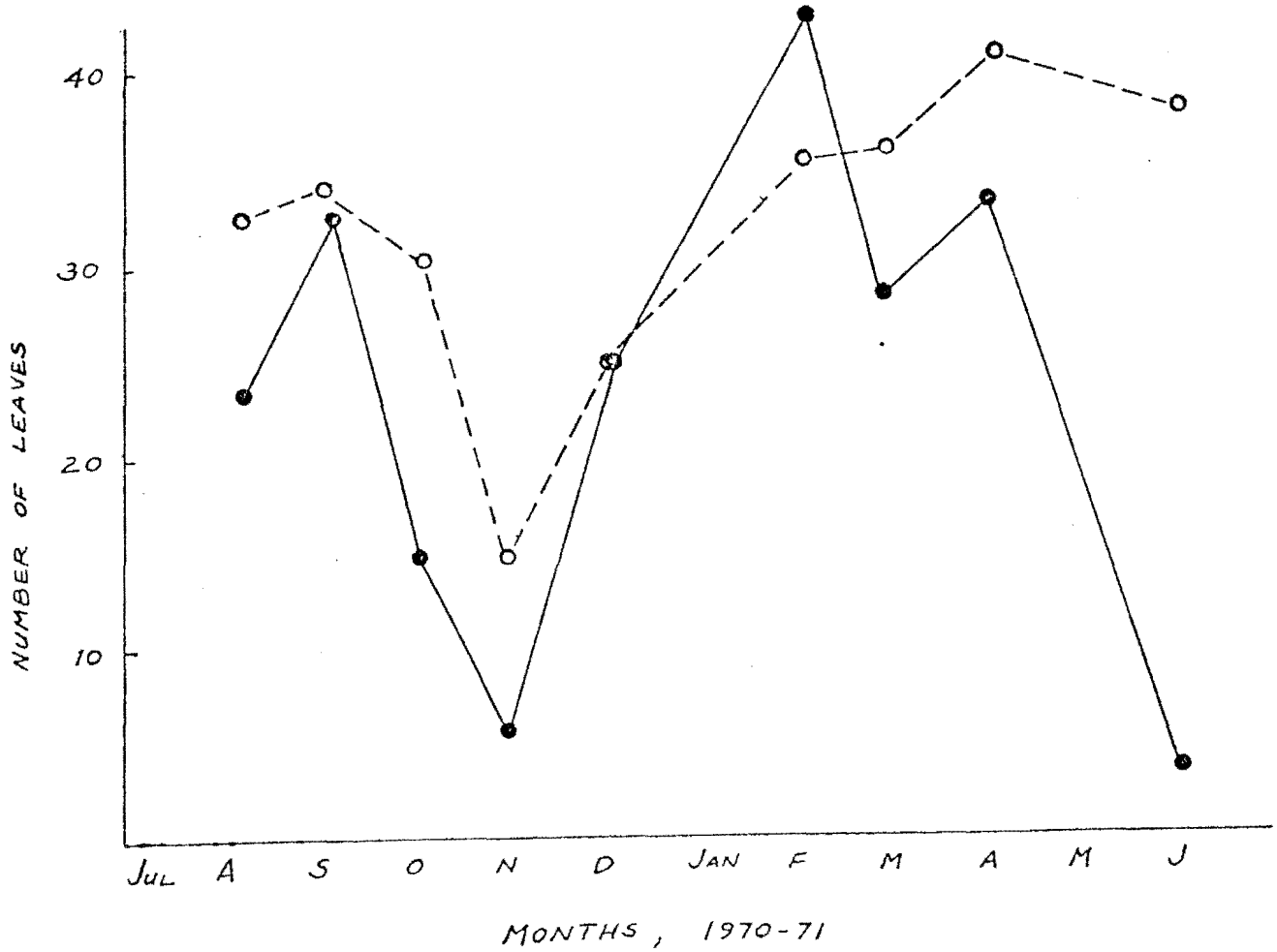

FIG. 5. Leaf production and leaf fall. An example of the total numbers of leaves produced and fallen from 10 branches of a polymorpha tree (plot 1, tree 17). (o——o)--leaf production. (o- - -o)--leaf fall.

Inflorescences that do not produce vegetative buds, closed inflorescences, occur especially on the more proximal buds of the newest flush or on older branches.

Many times I have noticed flowers on older branchlets in the variety incana, on branches up to 1.0 cm in diameter. Branch flowering as opposed to twig flowering is termed ramiflory and is an occasional development from buds that have been dormant for up to perhaps five years. Such ramiflory is most prominent when a tree has low retentiveness of leaves so that the flowers are borne on bare branches. A shrub in plot 4 was the only tagged specimen that exhibited ramiflory.

On young, vigorously growing incana shrubs, an inflorescence may develop from a terminal bud. Rock's (1917) reference to terminal inflorescences in the variety (species) macropus should be more properly termed acranthous inflorescences since they are borne from axillary buds near the top of the shoot.

Phenology of flowering and fruiting (varietal differences)--Figures 6 and 7 show the pattern of flowering for the study plots.

The peak flowering of variety polymorpha occurs in June and July in the plots and throughout the Koolau mountains on Oahu. Its form in the Waianae mountains flowers in August and September. The peak flowering in the variety rugosa is in September and October. All these trees have sharply delineated flowering times with one distinct peak each year. There was more intense flowering of polymorpha in 1970 than 1971.

The variety glaberrima on Oahu has a more prolonged flowering phase, from March through November. Individual trees had flowering periods one to five months in length with many of them peaking in August and September. With few exceptions there was but one annual peak for individuals. The variety glaberrima grows at the same sites as polymorpha, yet glaberrima had more intense flowering in 1971 than 1970.

The variety incana on Hawaii grows at all elevations from sea level to tree

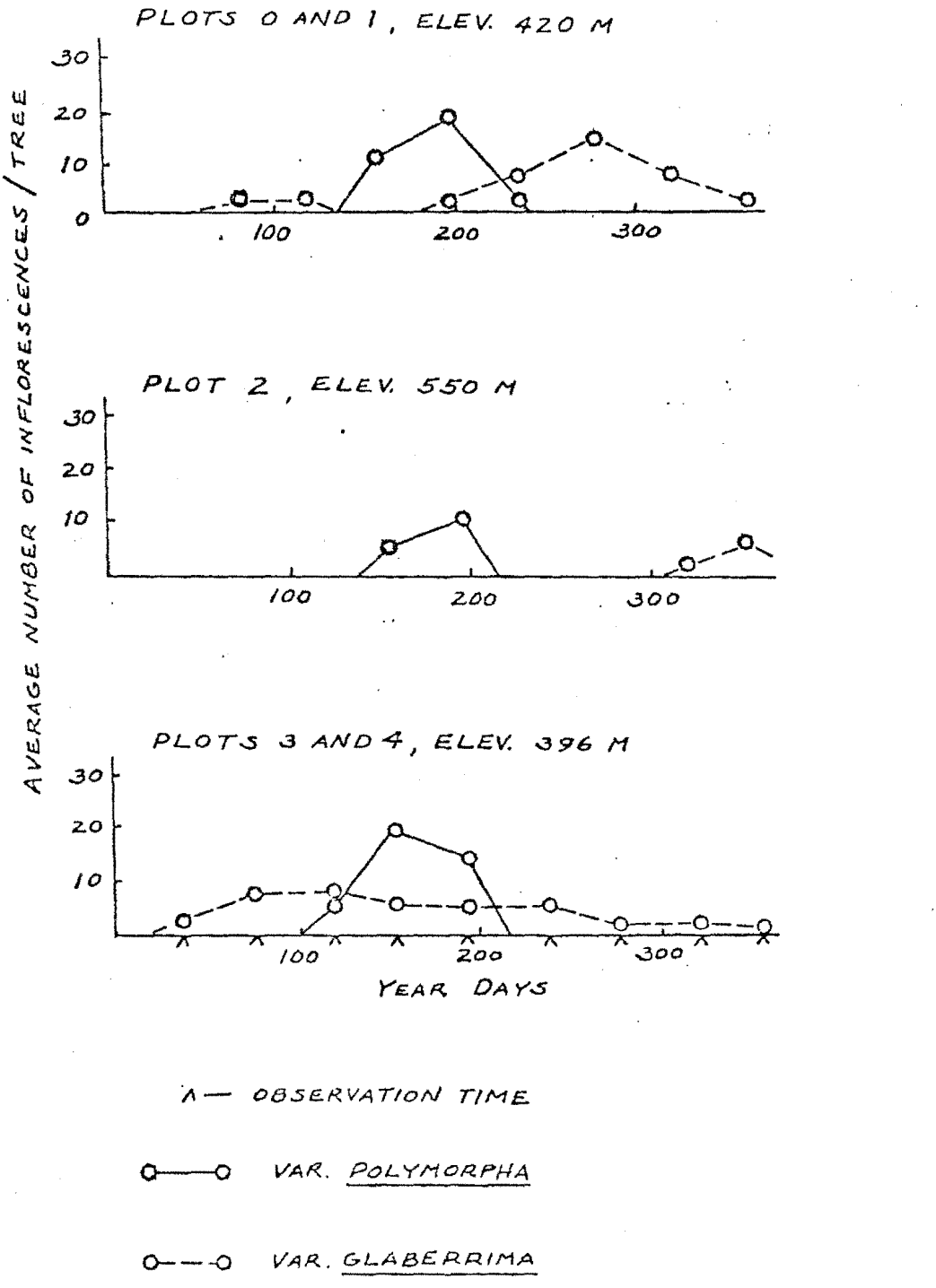

FIG. 6. The phenology of flowering in the varieties polymorpha and glaberrima. Average number of flowers in each plot at each observation time indicated.

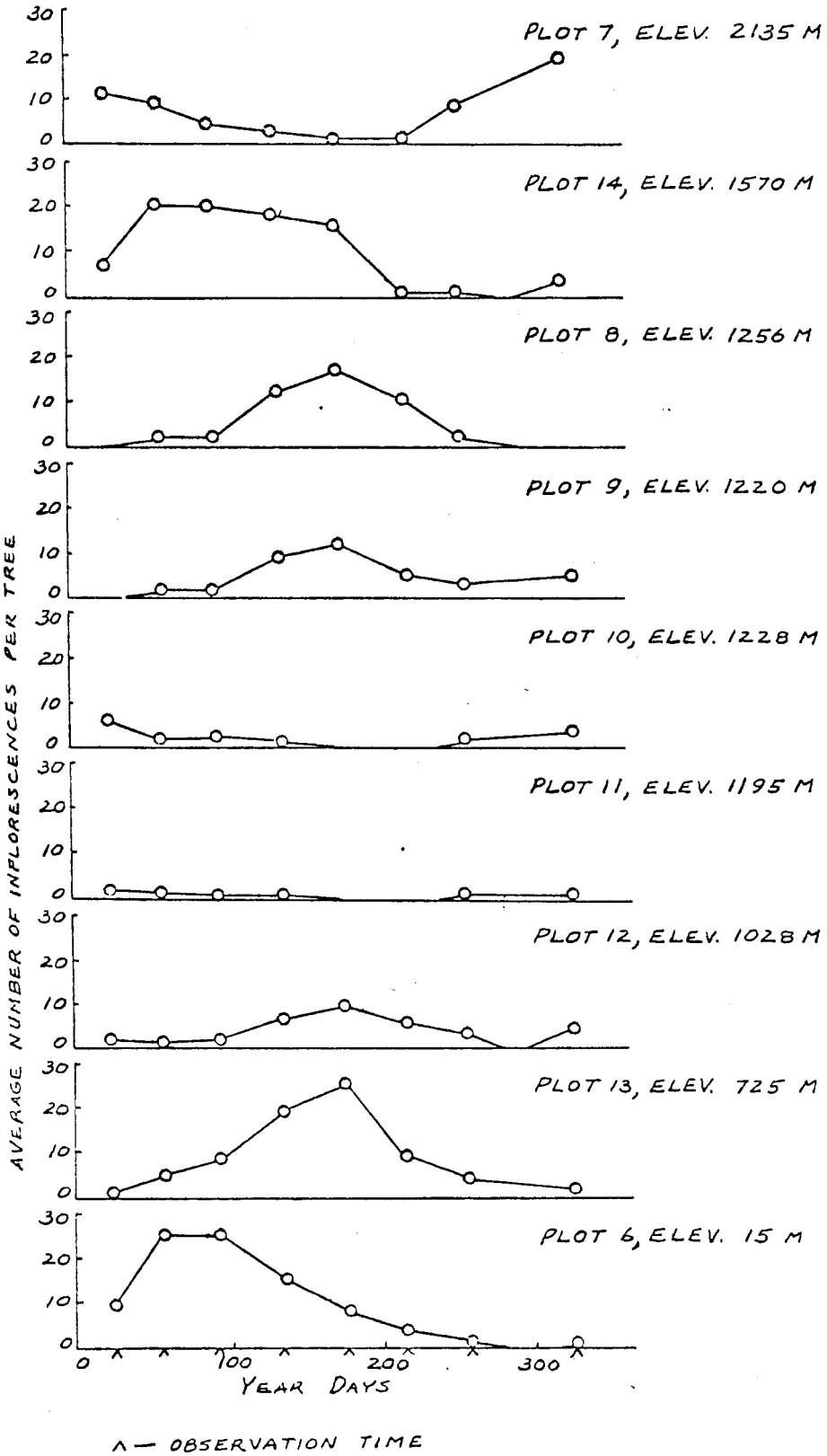

FIG. 7. The phenology of flowering in the variety incana. Average number of flowers in each plot at each observation time indicated.

line at 2600 m. Above 2100 m a form of incana with smaller leaves and more pubescence than the typical incana occurs. The flowering of this form and of another variety found only at high elevations, nuda, is most intense from November to January, the winter season. The winter peak also occurs at intermediate elevations in the rain forest, but flowering here is much less intense.

In the drier sites, the flowering peak of incana progresses from March and April near sea level to about June at 1200 m and above, suggesting some thermoperiodic triggering of flowering. The peak flowering of the variety macrophylla which predominates in the rain forest to the northeast of Hawaii Volcanoes National Park is March and April. In the rain forest areas there was less intense flowering in early 1971 than there was in early 1972. Conversely the drier forested areas had more intense flowering in 1971 than 1972. 1970 seemed to be a heavy flowering year also in the drier forests. Heavy flowering individuals tend to flower more heavily from year to year than less intensely flowering individuals.

Insect attacks--Heavy insect attacks on flower buds particularly by gall-forming psyllids greatly reduced flowering potential. Varieties polymorpha and rugosa are immune to their attacks. Certain trees of glaberrima, incana, and macrophylla are heavily damaged. Yet aside from these attacks, about 60 per cent of all the flowers, 844 out of 1415, on tagged branches did not set fruits.

Fruit ripening--Fruit ripening takes from 4 to 12 months, and since flowering most often occurs in spring and summer, fruit dehiscence and release of seeds occurs in the fall and winter. There are no direct relationships between time of ripening and elevation or temperature differences. The size of the fruit capsule also has little effect. In the variety incana for instance fruit ripening took the same length of time, 10 months, over a broad altitudinal range.

Trunk Growth

Circumference measurements--The basis for trunk growth information is the circumference measurement data for individual trunks. From these individual data, TABLE 5, the average daily change in each plot is given. The changes in circumference in mm for each stem from each measurement to the next were averaged on a plot basis, were divided by the number of days between observations and then were multiplied by 1000 to convert to micron (μm) units. A number of -15, for example, would mean that the trees decreased an average of 0.015 mm (15 μm) per day during the period in question. On the right hand side of TABLE 5 is the overall average daily increment for the plot for the entire study period of one year or longer. The daily increment is simply multiplied by 30 to calculate the values in TABLE 6. The annual per cent increment was calculated for each tree, and these percentages were averaged for the plots. The annual per cent increment for plot 10, 0.15 per cent, is positive while the 30-day increment is negative because those trees having a net increase had a greater percentage increase than those that had a net decrease on an annual basis. This also explains why the annual per cent increment values are not proportional to the 30-day increment values in TABLE 6.

Average per cent annual increment in each circumference size class, 101-200 mm, 201-300 mm, etc., is based on observations made over 12 to 17 months. The values are converted to an annual basis by multiplying the total increment by 12/n months (FIG. 8). The number of trunks in all size classes was 89 on Oahu and 132 on Hawaii. With increasing size and age the average annual per cent increment decreases.

To summarize the data on trunk growth: On Oahu, the variety polymorpha (all plot 2) was generally faster growing than variety glaberrima (most plots 0 and 1) except for those trees growing on the drier sites (plots 3 and 4) that grew

TABLE 5. Average daily change in circumference (μm) by plot. Average daily change between times of measurement and average daily change for the whole period (overall), one year or longer, are given.

Plot	Year day 1970							1971										Overall
	172	190	230	260	288	316	343	020	042	078	117	142	154	190	212	252	287	316	
0		-67	-52	-25	52	26	94	-5	11	1		0			7		9		4.25
1		0	-88	15	49	-21	62	-15	10	-1		29			4		20		5.3
2			-61	81	-19	62	25	-7	30	6		15			10		10		14.6
3						37	36	62	-46	27	0		10	7		13	53		19.9
4						43	30	-8	-10	14	26		30	0		11	13		14.9

TABLE 5. (Continued) Average daily change in circumference (μm) by plot

Plot	Year day 1970 343	020	042	078	1971 117	142	154	190	212	252	287	316	1972 007	080	Overall
				11	2		26	30	11		51	47	35		26.6
	-22		-79	48	-10		25	-16	12		-4	35	14		3.0
			35	-24	90		-20	28	35		32	30	43		27.7
	18		10	-12	15		31	43	6		31	15	6		16.3
			-27	0	-7		-10	24	0		27	-3	-7		-3.0
	6		16	12	-7		0	56	22		27	4	0		13.6
	34		0	50	60		14	37	29		41	21	21		30.7
	83		-33	-25	20		-78	108	29		19	-12	0		11.1
				22	51		-60	51	27		29	33	17		21.3

TABLE 6. Trunk growth, plot averages. Averages are based on all the measured trunks in each plot. Average foliage density is the average of all trees' densities based on a scale of 1 to 6 from thin to dense foliage crown. Average 30-day increment is derived from average daily increment for each plot. Average annual per cent increment is the average of per cent increments for each trunk measured in each plot.

Plot	Elev. (m)	Average circumf. (mm)	Average 30-day increment (mm)	Average annual % increment	Average foliage density
0	420	619	0.13	0.29	4.3
1	420	646	0.16	0.08	4.6
2	550	413	0.44	1.17	3.8
3	396	640	0.60	1.31	4.8
4	396	343	0.45	2.06	4.7
6	15	564	0.80	3.06	4.8
7	2135	787	0.09	0.83	5.2
8	1256	1425	0.83	1.28	4.3
9	1220	507	0.49	1.55	2.9
10	1228	274	-0.09	0.15	4.3
11	1195	607	0.41	0.70	3.6
12	1028	511	0.92	2.27	5.9
13	725	1700	0.33	0.20	4.2
14	1570	1207	0.64	0.99	5.1

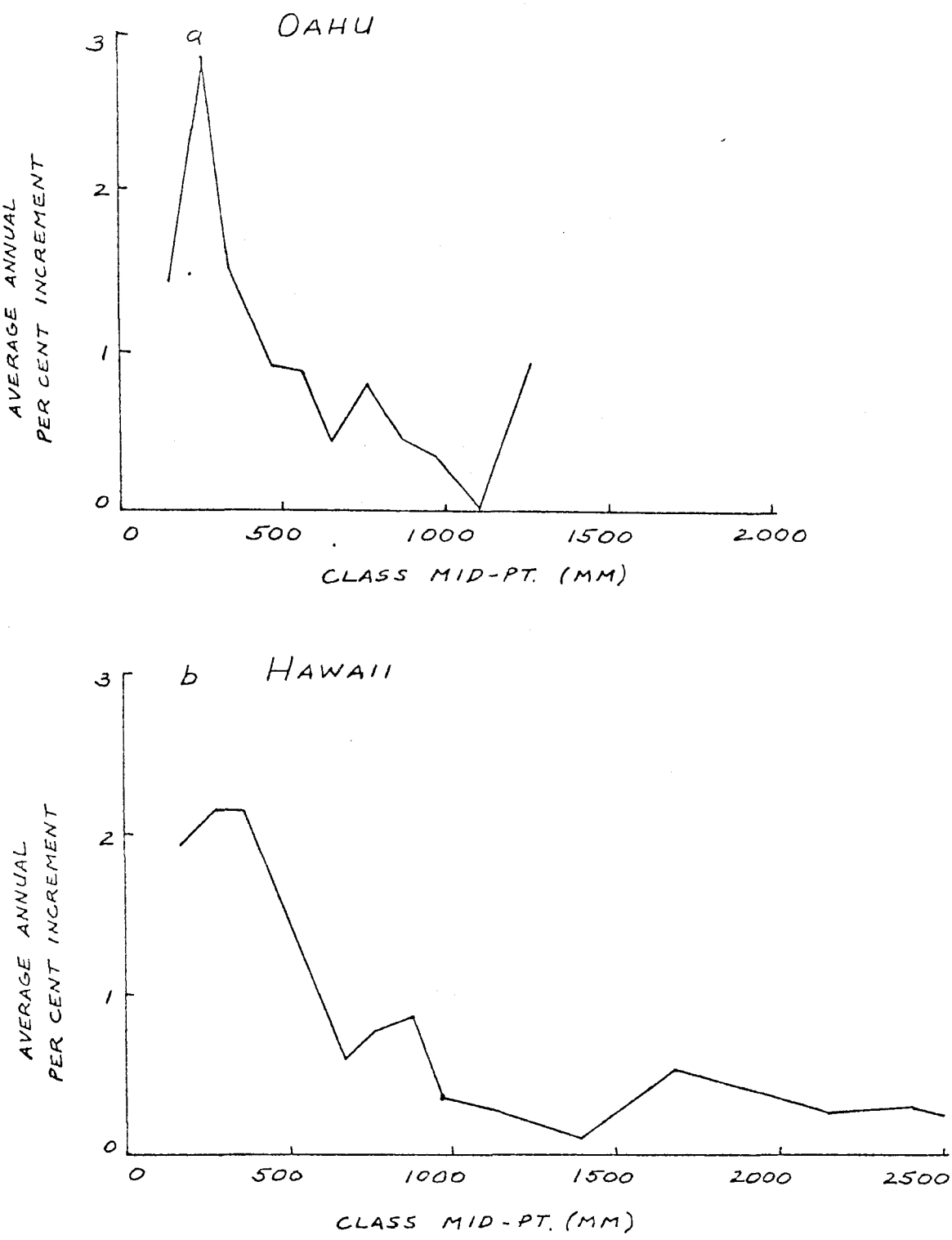

FIG. 8. Average per cent annual increment per size class, mm circumference. Classes are 101-200 m, 201-300 mm, etc.

comparably fast, 1.31 and 2.06 per cent per year. On Hawaii, the most rapidly growing trees were near sea level. Substrate conditions are not correlated with trunk growth rates. The most rapidly growing trees of incana at higher elevations were found both on a fairly recent aa lava flow plot 14, on a pahoehoe flow with recent thin ash plot 12, and on thick ash in a kipuka, a relict area surrounded by more recent lava flows plot 8. One tree in the last mentioned area grew 35 mm in circumference in one year. The trees in the wettest areas had slower growth than those in drier areas. Most trunk growth on Oahu occurred from October to December, most on Hawaii from July to November, after the flowering peaks in most trees.

Plots 1, 3, 9, and 11 have their average daily change in circumference graphed along with the growth of one fast growing trunk in each plot. Monthly rainfall data are also given (FIG. 9, 10, 11, and 12). Average growth in the plots is not correlated with rainfall.

The percentage of trunks growing more than 4 mm during the time measured is given in TABLE 8. Plots 8 and 12 had the highest numbers of fast growing trunks. They are similar in having summer-dry climates, but plot 8 has deep soil and plot 12 shallow soil. Plots 10 and 13 had the lowest numbers of fast growing trunks. They are not comparable as to climate, substrate or size class (TABLE 1).

Only several repeated measurements can show overall trunk growth. The negative changes do not necessarily show the cessation or even slowing of cambial activity. These could be related to the amount of hydration of the wood or bark. Small positive and negative changes occurred simultaneously in different trunks of the same tree, and both trends often occurred within a plot.

There was no correlation of monthly rainfall data and average monthly increment of a plot. Data were available for two neighboring weather stations on Oahu and four on Hawaii. Daily rainfall data were only available near plots 6 and 10.

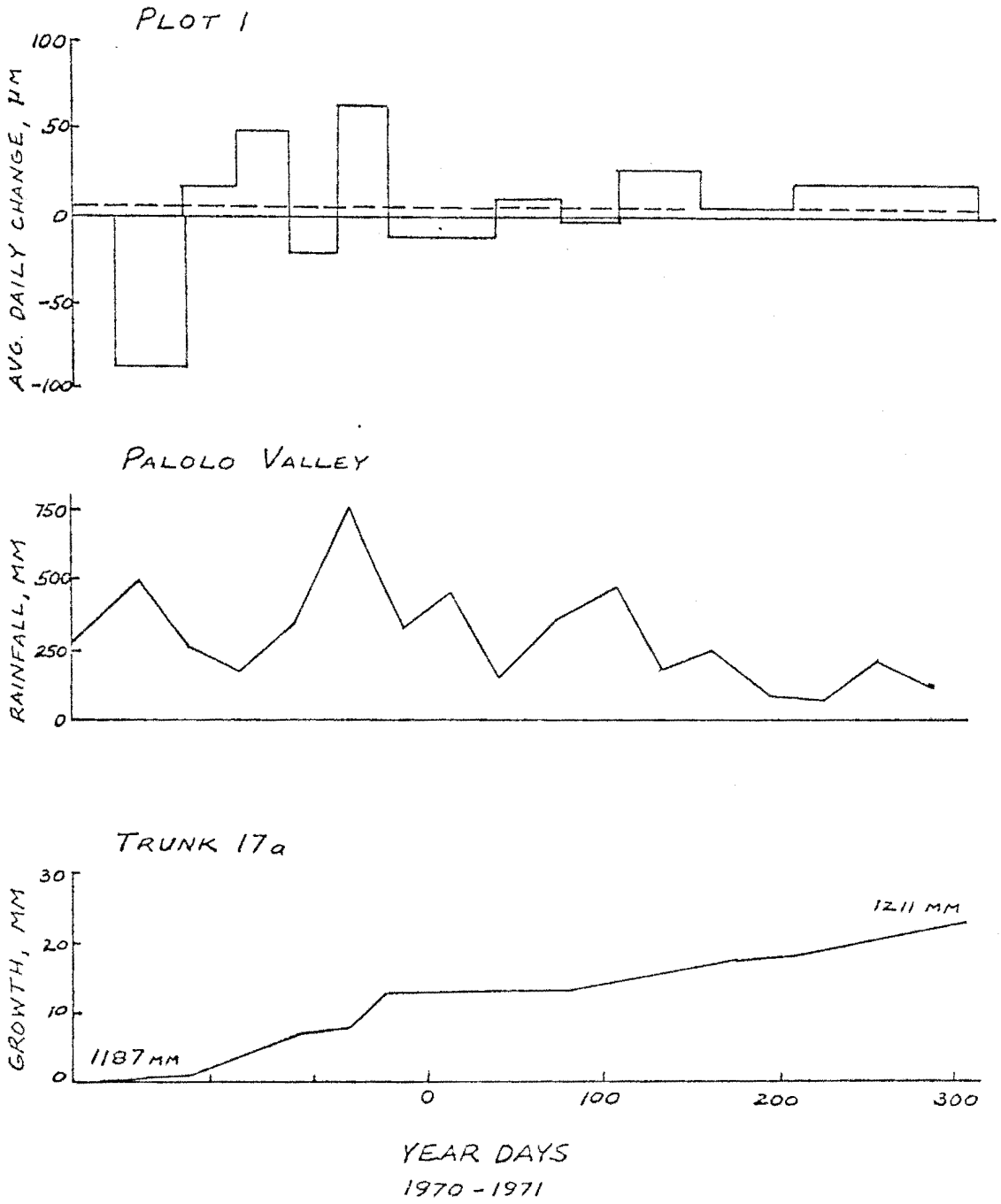

FIG. 9. Relationship between average daily change in circumference (µm) in plot 1 and rainfall. Also shown is the trunk growth of a fast growing trunk of variety polymorpha in the plot. There is no correlation between rainfall and growth.

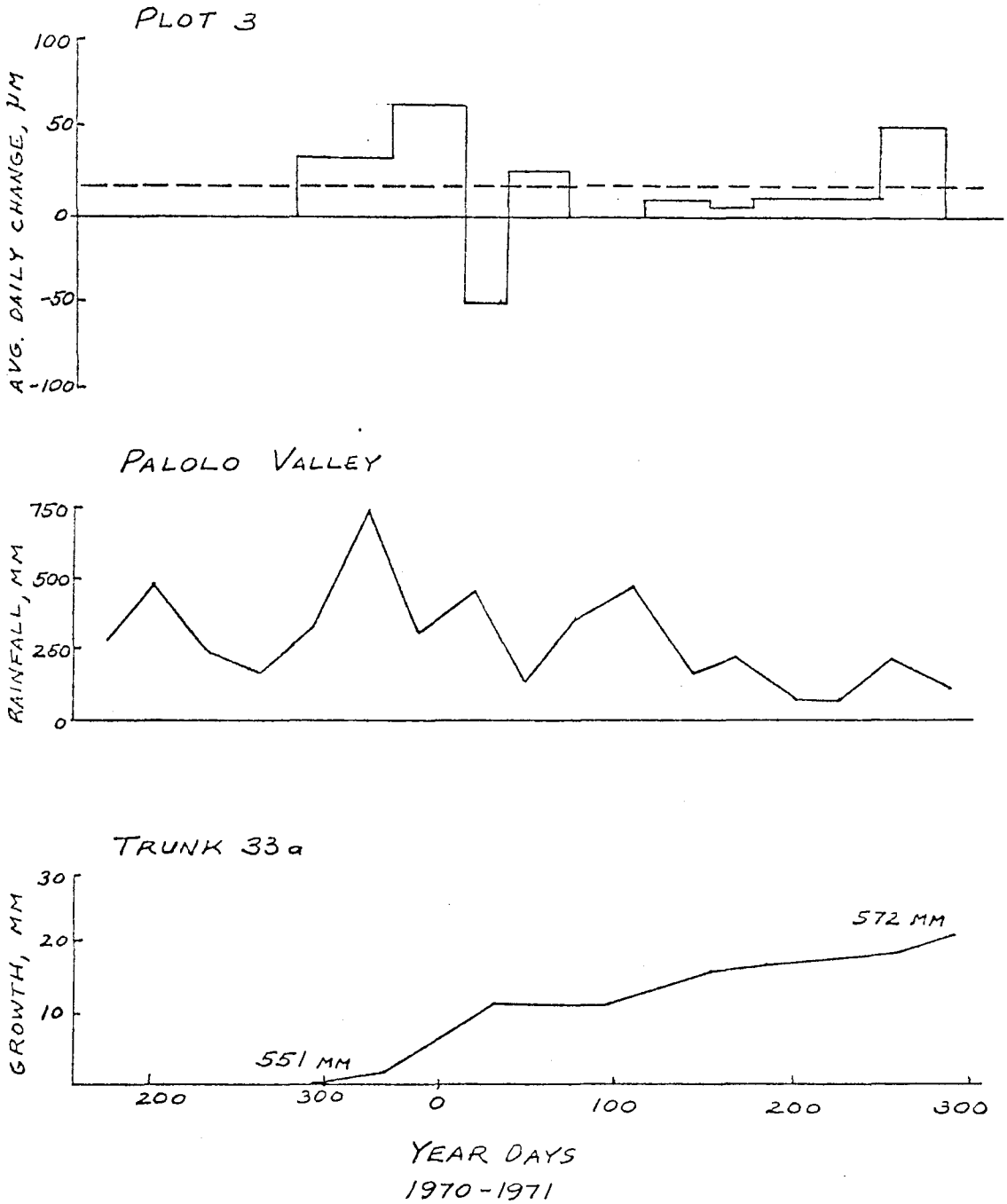

FIG. 10. Relationship between average daily change in circumference (µm) in plot 3 and rainfall. Also shown is the trunk growth of a fast growing trunk of variety glaberrima in the plot. There is no correlation between rainfall and growth.

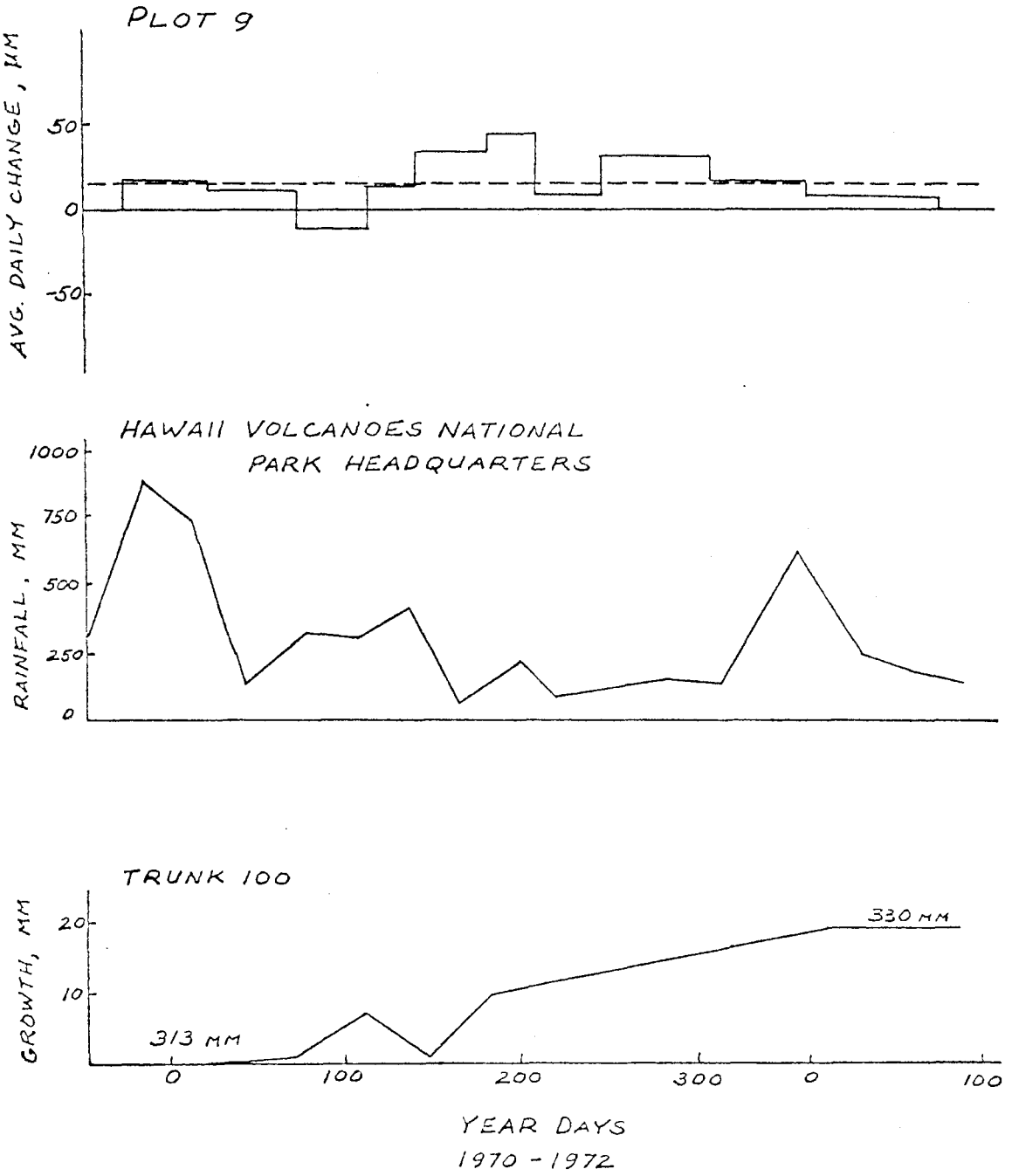

FIG. 11. Relationship between average daily change in circumference (µm) in plot 9 and rainfall. Also shown is the trunk growth of a fast growing trunk of the variety incana in the plot. There is no correlation between rainfall and growth.

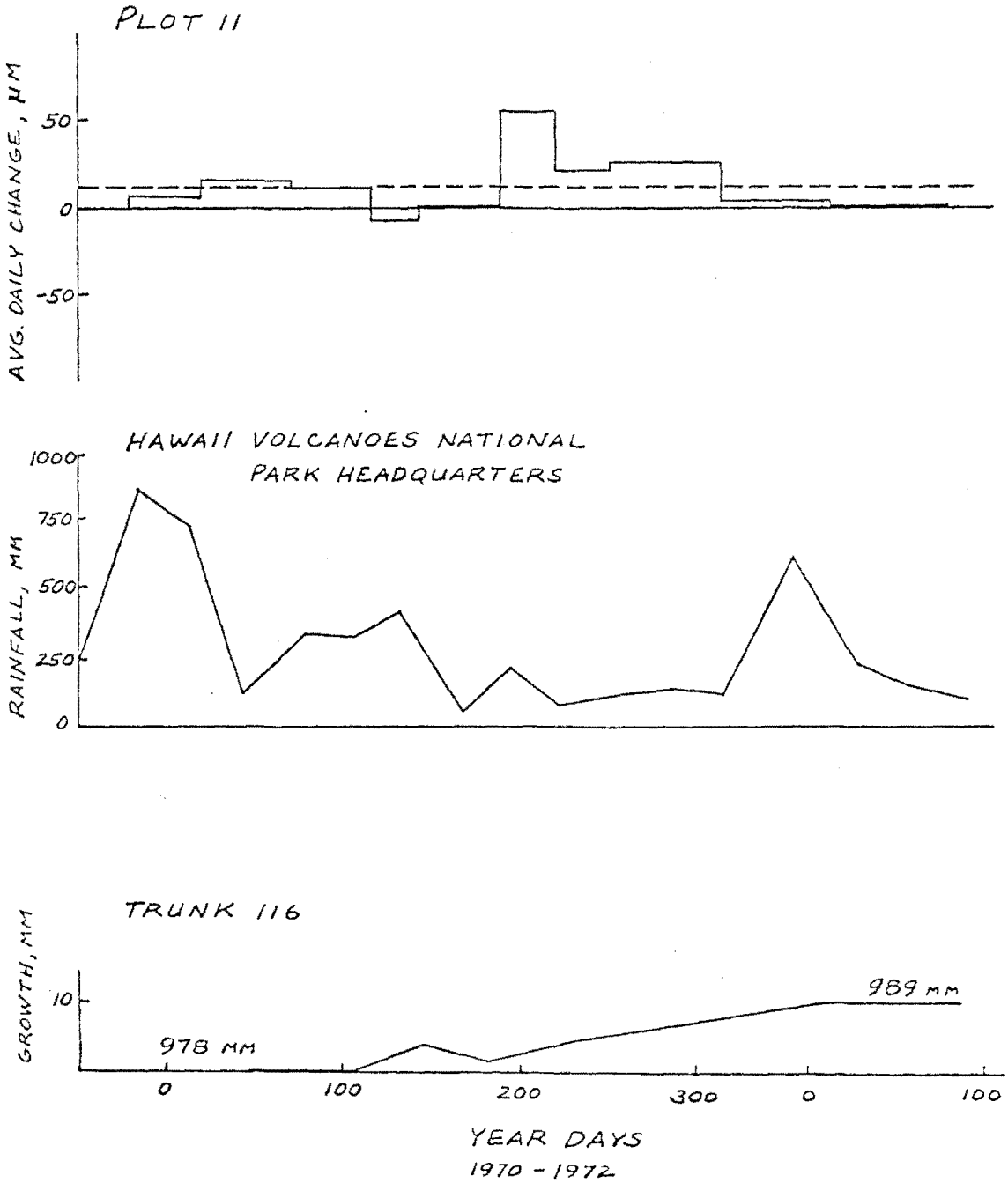

FIG. 12. Relationship between average daily change in circumference (µm) in plot 11 and rainfall. Also shown is the trunk growth of a fast growing trunk of the variety incana in the plot. There is no correlation between rainfall and growth.

Plot 10 represented the slowest growing trees in the study, 0.15 per cent average annual increment, while plot 6 the fastest growing, 3.06 per cent. Comparison of daily rainfall trends with increments for plots 6 and 10 showed that not a single tree consistently increased or decreased coincident with the previous 30 days' rainfall pattern.

The plot description table (TABLE 1) indicates that no two plots are "identical" in climate and substrate conditions, so one must be careful in generalizing. The fastest growing trees occurred in the lower elevation, xeric to mesic, open stands, while slowest were in higher elevation, more hydric, closed stands. Eggler's (1971) work offers a basis for comparison, although none of our Hawaii Volcanoes National Park study sites were in common. His Fern Forest study area, elev. 860 m, is similar to my plot 11 and his Sadleria-Metrosideros forest study area, elev. 854 m, is analagous to my plot 10. They were apparently more vigorous stands than mine since they were his most productive stands, measured in terms of biomass. Converting his data to 30-day circumference growth, I get values that are similar to mine (TABLE 6). Rather than duplicating his TABLE 3, "Average radial increment in mm, Metrosideros trees in 8 acres, between July 15, 1966 and Aug. 20, 1968.", I give the range of converted values: 0.10 mm/30 days to 1.32 mm/30 days. His Fern Forest average (1.32 mm) exceeds the highest value for my plots (0.92 mm). In his study he found that bole or trunk increment converted to mass was 16.8 times that of leaves plus short twig production in the Fern Forest compared to only 0.13 times (1:7.8) in the open lower Keomoku (sic) flow.

The general appearance of a stand gives no indication of the growth rates of individuals. For example, Rajput (1968) states that there is more vigorous growth on aa than pahoehoe substrates. The trees on pahoehoe in his study tended to be narrow crowned with some die-back. Grass cover was said to compete with the trees for available water. These trees did not look vigorous and their presence in an

open stand led him to believe that there was poor growth. My plot 6 trees near the coast were in such a stand and had such an appearance, but they were rapidly growing trees. The density of the stand cannot always be related to growth rates. I would predict, though, that the density of the stand can affect later growth rates and the eventual size of the tree. An open stand being more exposed to desiccating winds as in plot 6 could result in a smaller limit to the mature size of the tree.

There are other indirect indicators of growth rate besides circumference measurements. The bark can be an indicator (Wadsworth, 1953). Since Metrosideros has exfoliating bark, one would expect that rapidly growing trees in moist conditions would be free of heavy growth of lichens and mosses since there must be a stable substrate for good epiphytic growth. Under suitably moist conditions, as in plot 11, some of the slowly growing trunks are coated with epiphytes.

The thickness of bark (discussed in the next section) is as much a function of climate as growth rate and size class. In the same variety, trees in drier climates develop thicker bark than those in wetter climates. Smooth long bark scales, loosely or firmly attached are often found on rapidly growing trees.

In the larger size classes, small dark gray scales indicate long persistence of the outer bark and are a sign of slow growth. The most rapidly shed bark reveals unoxidized, reddish-brown bark beneath. The darker or duller gray the color becomes, the older it must be. In areas with heavy infestation of sooty molds, however, even rapidly growing bark can be darkened.

In smaller, rapidly growing young stems up to many centimeters in diameter, the bark is very smooth, not deeply cracked, and flakey pieces of cortical tissue are adherent to the outside widely separated from each other.

The best indicator of trunk growth is the density of the crown. A dense foliage crown indicates a rapidly growing tree, no matter what size. This is on a

relative basis between individuals within plots. For example, fast growing trees 17 and 33 had foliage densities of 6 and 5 (6 is most dense). Likewise, trees 100 and 116 had densities of 4. All these densities are larger than the average for the plots (TABLE 6). When average density of crowns is compared to average growth, there is no correlation (TABLE 8).

Long flushes with long internodes are correlated with rapid trunk growth. In larger trees, however, the long flushes may still be produced, but the crown has become too thin and too distant from the trunk to sustain a rapid increase. For example, tree 61 with long flushes had approximately 6,000 leaves and 303 mm circumference while tree 137, also with long flushes, had about 55,000 leaves and 2953 mm circumference. These are roughly the same proportions, but photosynthate must supply a much greater area and mass of developing secondary tissues in tree 137. Tree 61 grew over 3 cm in circumference in one year, and tree 137 shrank.

Cambial activity--The cambium of Metrosideros in all Hawaii and Oahu sites tested is continuously active, and was active in every block sampled. It is even active in unhealthy trees, those with heavily galled leaves and twigs, with considerable dead branches, and with no measurable increase in circumference.

The sapwood exposed during the block or strip sampling procedure is very light brown to pinkish white in color and is slippery to the touch. Both the exposed external tangential surface of the sapwood and the exposed secondary phloem facing it in the portion of the inner bark removed have a fluted appearance.

Thickness of the various tissues as exposed by the block method are given in TABLE 7. These figures do not necessarily represent the typical situation at each site, but only a particular specimen. The sapwood-heartwood color transition refers to whether the wood gradually becomes darkened or whether it is abruptly formed within a millimeter or two. The periderm was thickest at drier sites, for example, plot 6 had remarkably thick bark in relation to average trunk diameter.

TABLE 7. Tissue thicknesses of the outer portion of the trunk. Measured from 5 block samples for cambial activity in each plot. Sapwood-heartwood color transition is either gradual changing in several mm of radius or abrupt having a color change in 1 to 2 mm.

Plot	Altitude (m)	Trunk diam. (cm)	Bark		Sapwood (mm)	Spwd-htwd trans.
			Periderm (mm)	Phloem (mm)		
1	420	36	2-3	7	10	grad.
2	550	17	3-4	3	2-3	abru.
3	396	22	2	4	3-5	abru.
6	15	19	10	6	5	grad.
7	2135	32	8	3-9	6	grad.
8	1256	47	10	5	3	grad.
9	1220	30	2	4-8	3	grad.
10	1228	14	1	6-8	20	grad.
11	1195	23	2	4	?	grad.
12	1028	24	1	4	6	grad.
13	725	58	6	4-8	2-3	grad.
14	1570	34	12	6	6	grad.

TABLE 8. Estimated ages of trees, of fastest growing trees in plots.

Plot	Avg. circum. (m)	Percentage growing more than 4 mm	Range of ages (years)
0	619	50	38 to 165
1	646	40	43 to 185
2	413	44	23 to 105
3	640	60	27 to 101
4	343	58	23 to 103
6	564	75	10 to 119
7	757	38	56 to 240
8	1425	87	29 to 183
9	507	56	21 to 162
10	274	27	31 to 50
11	607	58	39 to 141
12	511	93	15 to 125
13	1700	33	52 to 230
14	1207	63	15 to 479

Small branches less than 2 cm diameter were sampled using the strip method on the Palehua-Palikea trail in the Waianae mountains on Oahu. The cambium was inactive in branches lacking active vegetative growth while it was active in the trunk. The bark could be removed after strips were incised and pried with a knife, but the cambial zone was not smooth and patches of phloem still adhered to the sapwood. This test was not conducted on the trees that I regularly sampled for trunk cambial activity since they did not have low branches which could be sampled.

The ease of slippage of the bark is a semi-quantitative method for determining rates of cambial activity. When I did find a sample where all of the bark in the block did not readily detach from the wood at the cambial zone, and this was often only a millimeter or so wide vertical strip, I would take another sample from the trunk at that time. It would always be active. Every cambial sample removed from a trunk by the block method was judged to be active.

The cambial sampling method of removing a bark-cambium-wood block does not determine the rate of cambial division because it is not repeatable at the same spot. It is impossible to get actual comparable counts of cells derived per certain area of cambium. An indication of the slow rate, however, are the small numbers of undifferentiated derivatives found on either side of the cambium, generally on the order of one to three cells.

Trunk growth in Hawaiian Metrosideros is relatively slow when compared with other woody species, both native and introduced (Carlson and Bryan, 1959). The tendency for Metrosideros to produce much reaction wood indicates that the rates of xylem production vary throughout the trunk, up and down the axis, and around the circumference at the same level. This is again a reason to use circumference as a measure of trunk growth since it can reflect some of this variation. There was no cambial activity as determined only by the strip method in both the small

branches and in the aerial roots either in times of vegetative interphase or after a few weeks drought. The lack of distinct cambial phenophases in the trunk could be due to the prolonged and over-lapping vegetative phases always supplying a hormonal stimulus to the cambium in the trunk from various parts of the foliage crown. Even when the sapwood was under water tension, when air could be heard being drawn into vessels while I was sampling, the cambium was quite active.

Age of the trees--From the circumference measurements it is possible for one to estimate the age of trees. The disadvantage of using only one year's data, as I am doing, is (1) that the data may or may not be representative of an average year's growth, and (2) the trees' past history is unknown, there being no growth rings in the wood. I am making the assumption that the growth is representative of the average.

The growth rate curve of circumference for most woody species is ideally represented by a curve that rises sharply, levels off, and finally falls. The actively growing trees belonging to any mature size-class are growing at more or less the same rate from year to year, under the same conditions, but at a lower percentage rate each year (FIG. 8). If a tree is actively growing it is presumably growing in a matter represented by an s-shaped cumulative growth curve, and on this basis extrapolations from the segments of the curve with the steepest slope can be made to get age estimates of the tree. If several years' data are available, there are better formulas for age estimates (Lojan, 1967).

To calculate the age of a tree, the annual increment, taken to be the annual rate, was divided into the last measurement taken:

$$\text{estimated age} = \frac{mm_1}{(mm_1 - mm_0)\ (yr^{-1})}$$

Since the plots may represent uneven-aged stands in differing size classes, no average ages for stands as represented by the plots are given (TABLE 8). The

range of estimated ages suggest that these are uneven-aged stands. Five trees were selected from each plot and the age estimate relative to size is given (FIG. 13). The average rate of growth for the rapidly growing trees in all plots was 11 mm circumference per year based on the linear regression line in FIG. 13. This value relates quite well with the 0.92 mm per 30-day increment found in the fastest growing plot (TABLE 6).

GENERAL DISCUSSION

Correlation of flowering and flushing--When flowering is directly compared and correlated month by month with average vegetative activity, few of the plots have any degree of correlation. An exception is that plot 7 does have a high negative correlation ($r = -.862$) between the values (FIG. 14). The flushing peak precedes the flowering peak by about three months. The other plots, however, have less clearly defined vegetative peaks or poor correlation of flowering and flushing as in plot 8 (FIG. 14).

The processes of development of flowers and flushes take similar lengths of time. Both types of buds take similar times to develop to bud break once they have differentiated. The flowering itself lasts about a month while the observable elongation may last two months or longer before the hardening off process. The likelihood that at each observation period newly opened inflorescences were counted on the tree was good because the time between observations was always at least a month, the maximum duration of flowering within any one inflorescence, but since the flushing process lasts a few months many if not most of the same flushes would be counted repeatedly. It may be invalid then to attempt to correlate flowering with flushing for either whole tree or plot data. The patterns become muddled.

The intensity of flowering is the total number of inflorescences during the study period per number of leaves on an individual specimen. Total numbers of

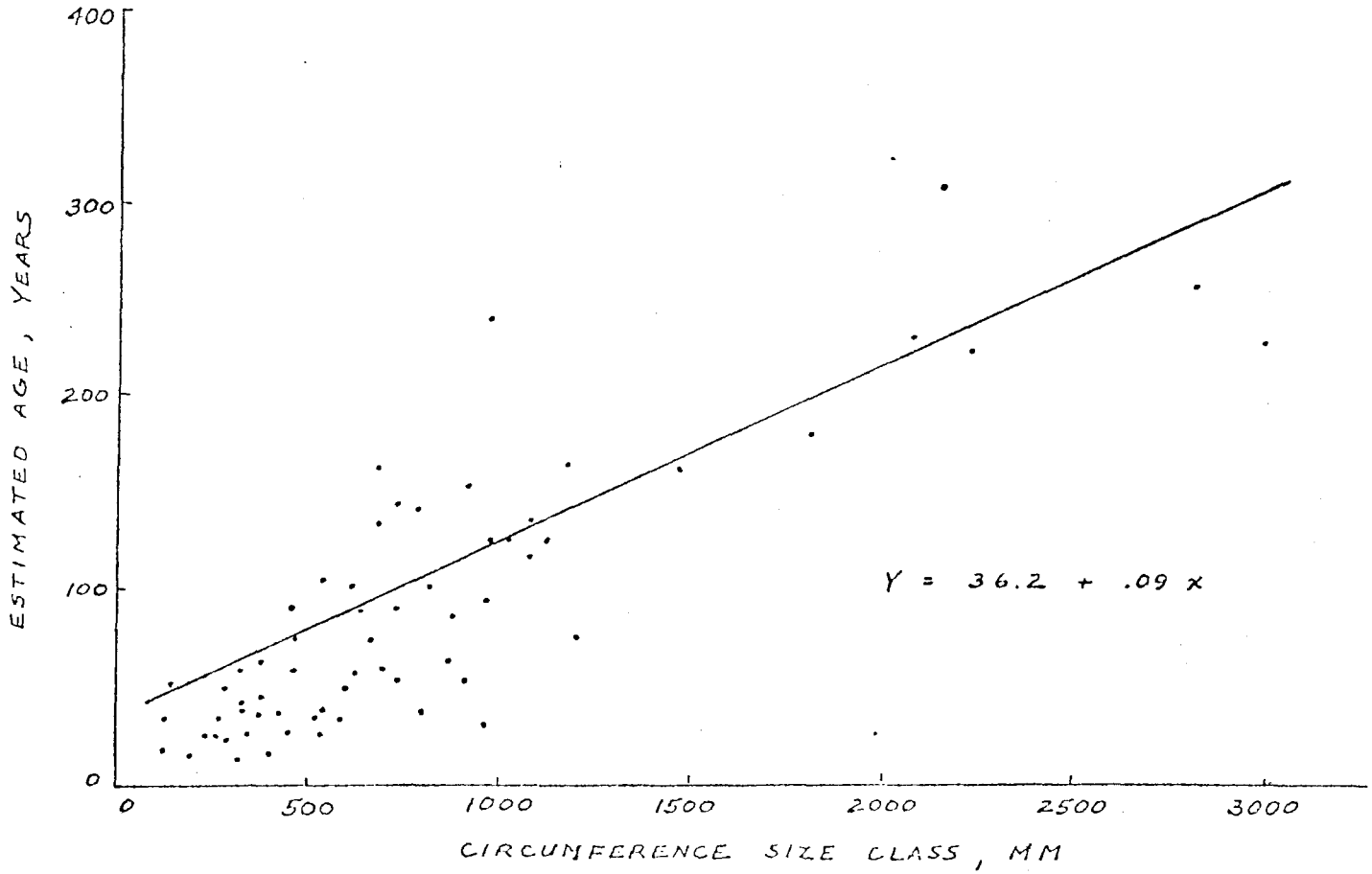

FIG. 13. Relationship between trunk size and estimated age.

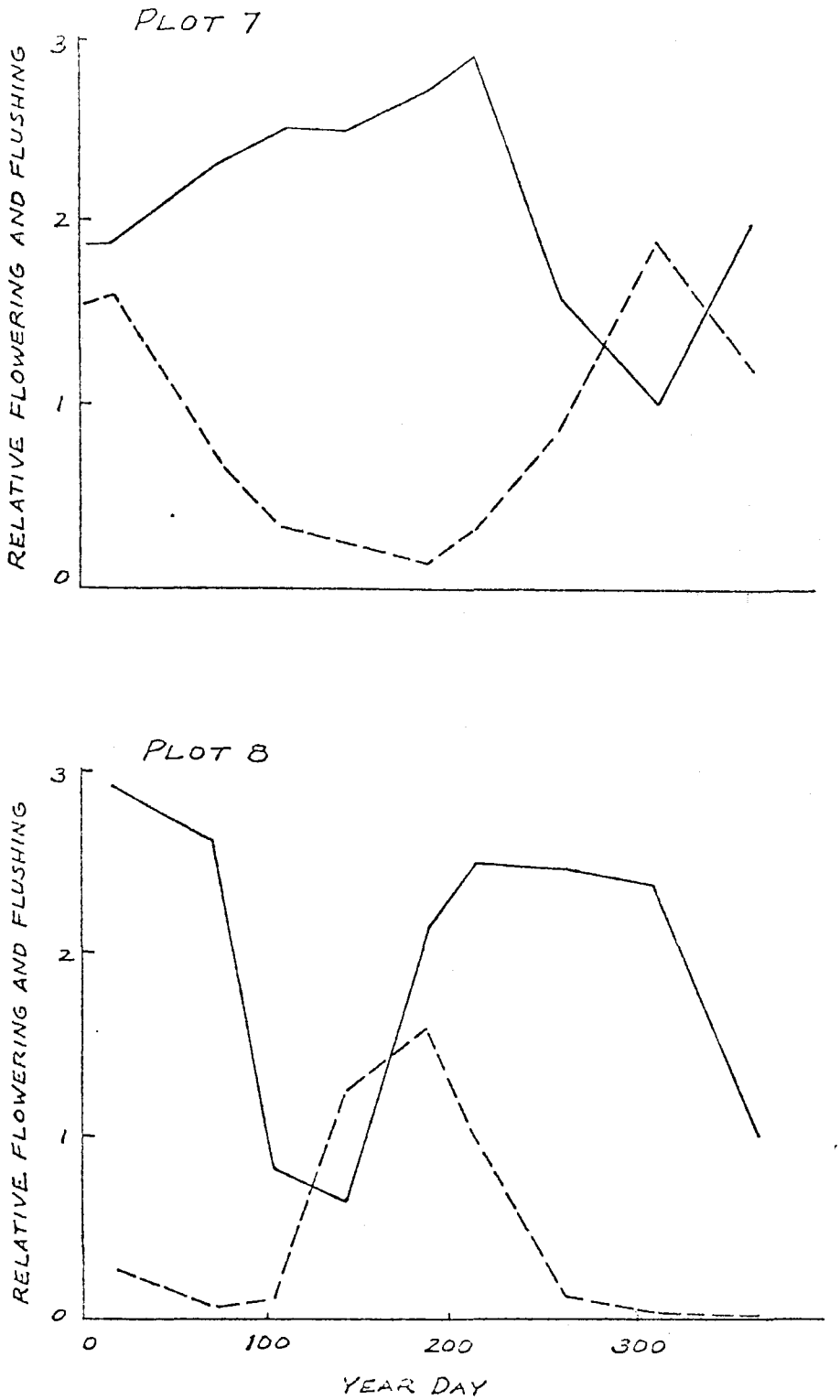

FIG. 14. Flowering and flushing in two plots; plot 7 (a) and plot 8 (b). Flushing (o——o) is averaged for all trees in the plot: 0--no flushing, 1--few flushes, 2--some flushes, and 3--many flushes. Flowering (o- - -o) is based on average number of inflorescences on all trees: 1--10 per tree, 2--20 per tree, and 3--30 or more.

inflorescences are used for calculating intensity because a lesser number of flowers over a long period may or may not be just as effective for reproductive potential as many flowers produced in a short time. It also directly relates reproductive growth to vegetative growth. The greater the intensity of flowering is, the less the numbers of buds involved in vegetative growth; however, two stands of Metrosideros having similar intensities of flowering might be quite different in appearance. One may have thinly foliated crowns and still produce the same proportion of flowers as a stand with thickly foliated crowns.

Flushing occurs at most times, with occasional peaks. Particular inflorescences will follow a particular flush, that is, they usually form on the new twigs and if not, then flowering on older branchlets occurs at the same time as flowering is occurring on adjacent new twigs. In the variety incana flushing and flowering are annual processes.

In varieties polymorpha and glaberrima flowering is also annual, but of only a few months' duration. In these varieties, more than one flush each year can occur. In this case there is competition in that axillary buds of recent flushes are forming more flushes and not flowers in that same year. The flowering season is thus curtailed. Individual branches form buds continuously throughout the year. The period that one bud development can follow another, flush on flush or flower on flush, can be less than six months to many months later.

The site of stimulus-response for the initiation of bud differentiation is apparently specific: the bud itself. In bud pairs one bud may develop into a flush and the other into flowers simultaneously. On a number of pseudo-dichotomous branches in the Footprints area of Hawaii Volcanoes Park, I have seen one bud of the pair form a twig, the other an inflorescence. These are followed by an inflorescence on the former twig and by a twig on the latter inflorescence. The formation of an inflorescence bud on another inflorescence is rare.

Regulation of phenophases--The timing of the vegetative phenophases is correlated with the rates of shoot development. In those varieties with no long interphases the new buds begin to develop just following the end of elongation.

The distal axillary buds are most likely to develop into either vegetative or reproductive branches. Both types can be formed and develop at the same time. The basic structure of an inflorescence and a vegetative shoot is the same, an axis with pairs of structures: in the case of the inflorescence two cymules in each pair, in the case of the shoot two leaves per pair. Both buds are forming determinate structures with approximately the same number of pairs.

The position of those buds that flush or flower is probably controlled by an inhibitory effect of the leaves. There is this evidence for the effect. Most varieties produce shoots with the leaves graduated in size from smallest at the tip or distal end to largest at the base or proximal end. The buds develop next to the smallest leaves. When ramiflory occurs or flushing from older branchlets, flushing usually occurs at nodes where the leaves have already fallen. One shrub produced very small-leaved flushes where the leaves were not sharply graduated in size. Flushes occurred from most of the nodal positions, infrequently from the sub-apical node. Thus there would appear to be a quantitative inhibitory effect, the larger leaves being more inhibitory than the smaller ones.

Correlation of flowering and flushing with climate--The rainfall data (FIGS. 9 and 11) show the general patterns during the study period. The availability of water and other limiting factors could possibly alter the growth potential and phenology.

Average temperature fluctuations from month to month are minor. Normal ranges are from 15° to 25°C. at the Oahu sites and 10° to 20°C. at the Hawaii sites. I did not have monitoring devices such as a hydrothermograph in the plots, so there are no continuous temperature records. Thermoperiodism is difficult to study in the field and to correlate with the flowering phenophase of Metrosideros

because particular temperature patterns at some point in time would be difficult to correlate with the later appearance of a certain inflorescence in a specimen that has a flowering phenophase lasting several months.

The fruiting phase is correlated with the wetter winter months in the summer-dry climatic zones. Most capsules dehisce in the fall and winter regardless of flowering time, explaining why fruit development may take from six months to almost a year before dehiscence. The capsules reach full size within a month of anthesis and remain this way until color change prior to dehiscence and seed release. In the tagged branches no newly dehiscent capsules were counted in April, June and July, and in the whole tree data none in August. Fruit dehiscence is accomplished in a shorter time than the total flowering phase. The advantage of having dehiscence and dispersal of seed in the wetter times would be the greater chance of germination and seedling survival. Seed germination is best with newly released seeds (C. Corn, personal communication).

Baldwin (1953) found that Metrosideros had increasing duration of flowering period with rise in elevation with a delay of the onset of flowering. My data confirm the prolongation of the flowering phase, and this could be attributable to the lower temperatures which slow processes. He saw differences in flowering on different adjacent substrates within the same climatic zone, yet "genetic differences may exist in the plants." The differing phenotypes accompanied by differing phenologies would indicate to me differing genotypes.

The trees in Hawaii Volcanoes National Park were chosen to compare phenological responses among individuals of the variety incana. As with the variety glaberrima on Oahu, the variation in form within the variety is accompanied by the variation in phenology. The casual assignment of a specimen to a particular form of a variety in a certain area may have to be changed because of its phenology once it is ascertained.

From observations made outside the study plots, incana has a spring to early summer flowering peak throughout the range below 1000 m or so in the south Puna, Ka'u, and Kona districts.

The varieties macrophylla and newellii are common in the wet climate of the north Puna and Hamakua districts on the east slopes of the island of Hawaii. Both have spring flowering peaks, and C. Corn (personal communication) and I have observed that they have shorter flowering times than incana. Some incana occurring in the rain forest do have a winter flowering peak, but I do not have enough observations to say whether this is true throughout its range in the rain forest.

Those specimens I have observed through two flowering cycles had different flowering intensities from one to the next, although the intensely flowering ones continued to flower more than the less flowering ones in the subsequent flowering peaks. There does not seem to be the phenomenon of "alternate-bearing" found in some woody species.

Correlation of flowering and pollinators--Sympatric varieties such as polymorpha and glaberrima have chronologically distinct floral phenophases which could allow for reproductive isolation. Although complete cross-pollination experiments have not been conducted, concomitant flowering within one variety may suggest that some trees have developed self-sterility barriers (Daubenmire, 1972). Propagation of a variety or form would depend on between tree coordination of flowering to allow for cross-pollination between individuals. With this capability to out-cross, an individual of one variety could have the capability to cross with another individual of another variety. Apparent hybrids are recognizable in the field. To maintain separate varieties then would require a type of reproductive isolation. If there is free mixing between Metrosideros varieties best adapted combinations of characters that have extended the adaptive range of the species could be altered.

Intervarietal competition for pollinators could be keenest between taxa

having large populations and those taxa with small populations. There is some overlap of flowering times of the morphologically distinctive varieties of polymorpha and glaberrima, but both have large numbers of individuals. There are no apparent hybrids between the two varieties. The variety rugosa, quite close to polymorpha morphologically, has a small number of individuals restricted to small sites along the mountain crest. The range of variety polymorpha extends down the ridges below the crest. Hybrid populations are found between the two varieties on Puu Konahuanui in the Koolau mountains but I do not know the phenologies of those populations.

Pollinators could have exerted selective pressures on the phenology of flowering in Metrosideros. The peak flowering occurring in the drier seasons of the year in many varieties seems to be of no particular advantage in relation to bird pollination. My observations are that the birds are not deterred from visiting the flowers by rain itself, although the nectar being quite exposed in the flower could be diluted by rain water and be less attractive to the birds. Many flying insects, on the other hand, sharing a role in pollination, could be ineffective pollinators in cloudy or rainy weather. The times of population peaks of native insect pollinators are unknown. Exotic bees are most active during the drier summer months. Whether there is preferential pollination by insects and birds of certain varieties or even certain colors is not known.

The differences between the early summer flowering of polymorpha and the fall flowering of rugosa in the Koolau mountains could have been selected by bird pollinators that could only visit and successfully pollinate the flowers of rugosa when the very strong winds along the crest and cliffs ceased. The trade winds are fairly constant during the summer. The variety tremuloides, the only variety that occurs on the steepest slopes in a variety of exposures, has varying flower peaks throughout the year, yet even here restricted populations appear to each have their

own flowering peaks, perhaps, at the propitious time for pollinators of a particular type.

Correlation between trunk growth and vegetative or reproductive activity--There was correlation between the time of flushing and cambial activity in the small branches but none between the apical portions and the trunk. These findings are similar to those in orange trees (Cameron and Schroeder, 1945). The flowering of heavily flowering trees was compared with trunk growth. One tree was selected from each plot and compared with circumferential growth of the trunk or trunks. There was no correlation. There was also no correlation between intensity of flowering in each plot and average growth in the plot.

CONCLUSIONS

Leaf and branch growth--Metrosideros trees in Hawaii have manifold growth. Budding, flushing, and leaf fall occur much of the time, each branch being on an independent cycle. Each branch grows intermittently and produces flushes having varying internode lengths and a gradation of leaf size. A terminal bud is lacking because the shoot apex aborts. The flushes are determinate and rate of elongation after bud break is related to variety, elevation and temperature, and the position on the tree or shrub. Vigorously growing trees, especially in seasonally dry areas, can form sylleptic shoots bearing numerous late leaves. Trees having this growth form have been considered previously as a distinct variety called imbricata. Without the production of sylleptic or epicormic shoots, a shoot system can consist entirely of determinate shoots.

Metrosideros has small sclerophyllous evergreen leaves that abscise gradually from the time of flushing to about three years. The average life span of a leaf is two years. There is no annual thinning out of the crown.

The variety incana has but one flush per year while the varieties glaberrima

and polymorpha have at least two, yet these patterns may be coincident with environmental conditions and not variety.

Reproductive growth--Flowering in most trees occurs annually on a branchlet or twig. Flower buds usually develop on the most recent flush after an interphase of a few months. The more irregular and prolonged the flushing pattern for a tree is, then the longer the flowering cycle. The period of peak flowering in a plot can last a few weeks to a few months. In variety incana at high elevation and in the humid-summer-dry transition zone the peaks were longer or less well defined. The intensity of flowering is greatest on the drier study sites.

On the island of Oahu, the varieties rugosa and polymorpha have the highest degree of within tree coordination of both vegetative and floral buds; consequently, the vegetative and reproductive phenophases are shorter and more pronounced than in other varieties. There is also a greater degree of between tree coordination, not only within the plots but over considerable areas. Chronologically distinct floral phenophases could allow for reproductive isolation of one sympatric variety from another. The maintenance of separate varieties has allowed Metrosideros to extend in habitat range.

Growth rates and life span--The growth rates in most mature specimens is relatively slow. Twigs elongate about 5 cm per year. The trunks grow about 2 per cent average annual increment in the smaller size classes down to 0.37 per cent in the larger ones. The maximum growth rates average 11 mm circumference per year. Age estimates indicate that the stands are uneven-aged.

There are no growth rings in Metrosideros and the cambium is continuously active in the trunks despite periodicity of growth in individual branches. The whole tree usually has vegetative growth throughout the year that could result in a continued stimulus to cambial activity.

Role of phenology in the ecosystem--Movements of animal populations and fluctuations

in population size within small geographical areas could be related to the times of flowering and flushing. Species of insects, for example, that are attached to or specific for one variety of Metrosideros may have life cycles coordinated with the phenology of flushing. The timing and duration of flushing could be related to the pattern of larval development. Leaf fall throughout the year particularly in areas of even rainfall distribution would imply a constant supply of food or cover to litter-dwelling organisms. Nectar and pollen feeders, whether they be pollinators or not, have a food supply from Metrosideros over much of the year in most areas because of the prolonged floral phenophases.

ACKNOWLEDGEMENTS

I especially thank Dr. Derral Herbst, Miss Carolyn Corn, Mr. Wayne Gagne, Mr. Joseph Meeker, and Mr. Larry Nakahara for their advice given during this study. Also, I would like to acknowledge the assistance of Dr. Charles H. Lamoureux, and Dr. D. Mueller-Dombois and the IBP ISLAND ECOSYSTEMS IRP which provided partial financial support.

REFERENCES

Baldwin, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepaniidae). Univ. Calif. Publ. Zool., 52:285-398.

Blumenstock, D. I. and S. Price. 1967. Climate of the states. Hawaii. U. S. Dept. Commerce. E.S.S.A. Climatography U. S. No. 60-51. 27 pp.

Cameron, S. H. and C. A. Schroeder. 1945. Cambial activity and starch in bearing orange trees. Amer. Soc. Hort. Sci., 46:55-59.

Carlquist, S. 1965. Island life. A natural history of the islands of the world. Natural History Press. Garden City, N. Y. 451 pp.

Carlson, H. K. and L. W. Bryan. 1959. Hawaiian timber for the coming generations. Trustees of the B. P. Bishop Estate. 112 pp.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J. Ecol., 60:147-170.

Dawson, J. W. 1967. A growth habit comparison of Metrosideros and Ficus. Tuatara, 15:16-24.

Dawson, J. W. 1968a. An analysis of flowers and fruits in New Zealand Metrosideros. New Zealand J. Bot., 6:43-55.

Dawson, J. W. 1968b. The vegetative buds of New Zealand species of Metrosideros. New Zealand J. Bot., 6:240-242.

Dawson, J. W. 1970. Pacific capsular Myrtaceae. 2. The Metrosideros complex: M. collina group. Blumea, 18:441-445.

Doty, M. S. 1967. Contrast between the pioneer populating process on land and shore. So. Calif. Acad. Sci. Bull., 66:175-194.

Eddinger, C. R. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanididae). Ph.D. Dissertation. Univ. of Hawaii. Honolulu. 212 pp.

Eggler, W. A. 1971. Quantitative studies of vegetation of sixteen young lava flows on the island of Hawaii. Trop. Ecol., 12:66-100.

Garrison, R. and R. H. Wetmore. 1961. Studies in shoot-tip abortion; Syringa vulgaris. Amer. J. Bot., 48:789-795.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evol., 21:620-637.

Koriba, K. 1958. On the periodicity of tree growth in the tropics, with reference to the mode of branching, the leaf fall, and the formation of the resting bud. Gard. Bull. Straits Settlem., 17:11-81.

Kozlowski, T. T. 1971. Growth and development of trees. Vol. 1. Seed germination, ontogeny, and shoot growth. Acad. Press, N. Y. 444 pp.

Lieth, H. 1968. Phenology in productivity studies. In: Analysis of temperate forest ecosystems. Reichle, D. E. (ed.), Vol. 1. Ecol. Stud., Anal. and Synthesis. Springer-Verlag, N. Y. 304 pp.

Lodewick, J. E. 1928. Seasonal activity of the cambium in some northeastern trees. N. Y. State Coll. For., Tech. Publ., 23:1-52.

Lojan, L. 1967a. Cálculo de la edad en ároboles sin anillos anuales. Turrialba, 17:419-429.

McClure, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. Malay. For., 29:182-203.

Rajput, M. A. 1968. Tree stand analysis and soil characteristics of the major vegetation cover types in Hawaii Volcanoes National Park, Hawaii. M.S. thesis, U. of Hawaii, Honolulu, Hawaii. 236 pp.

Rock, J. F. 1917. The ohia lehua trees of Hawaii. A revision of the Hawaiian species of the genus Metrosideros Banks, with special reference to the varieties and forms of Metrosideros collina (Forster) A. Gray subsp. polymorpha (Gaud.) Rock. Bot. Bull. Hawaii Board Agr. For., 4:1-76.

Schneider, H. 1952. The phloem of the sweet orange tree trunk and the seasonal production of xylem and phloem. Hilgardia, 21:331-353.

Skottsberg, C. 1944. Vascular plants from the Hawaiian Islands. IV. Acti Horti Gotoburg., 15:402-410.

Smathers, G. A. 1972. The recovery and succession of vegetation on the 1959 Kilauea Iki eruption site, Hawaii Volcanoes National Park. Ph.D. dissertation. Univ. of Hawaii, Honolulu, Hawaii.

Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Natur., 104:25-35.

Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. Oikos, 15:274-281.

Steward, F. C. 1968. Growth and organization in plants. Addison-Wesley, Reading, Mass. 564 pp.

Studhalter, R. A., W. S. Glock, and S. R. Agerter. 1963. Tree growth. Some historical chapters in the study of diameter growth. Bot. Rev., 29:245-365.

Swezey, O. H. 1954. Forest entomology in Hawaii. B. P. Bishop Museum, Spec. Publ. 44. 266 pp.

Wadsworth, F. H. 1953. New observations of tree growth in Tabonuco forest. Carib. For., 14:106-111.

Wardle, P. 1971. Biological flora of New Zealand. 6. Metrosideros umbellata Cav. (Syn. M. lucida (Forst f) A. Rich.) (Myrtaceae). Southern rata. New Zealand J. Bot., 9:645-671.

Wilson, B. F. 1970. The growing tree. Univ. of Massachusetts, Amherst. 152 pp.

TECHNICAL REPORTS OF THE US/IBP ISLAND ECOSYSTEMS IRP

(Integrated Research Program)

No. 1 Hawaii Terrestrial Biology Subprogram. First Progress Report and Second-Year Budget. D. Mueller-Dombois, ed. December 1970. 144 p.

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